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THE PALAEOONTOLOGY AND GEOLOGY OF DUNSINANE SITE, RIVERSLEIGH

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The stratigraphy, fossil assemblages and models of formation and post-depositional history of Dunsinane Site, on the western 'arm' of southern Gag Plateau, are described. The fossil vertebrate fauna most resembles the late Oligocene (System A) fauna of White Hunter Site. Rich, exceptionally preserved invertebrate and plant (twigs, leaves, reproductive organs) assemblages occur in nodules of iron oxide-rich fluorapatite and as fragments derived from these nodules and appear to have been preserved by early diagenetic microbially-mediated phosphatisation. The sediment is most likely lacustrine and may directly overlie Precambrian sediments. Erosion of overlying sediments and severe chemical weathering may have led to development of the surface lag of insoluble residue which includes phosphatised bone, nodules and other fossil fragments. Relationships of the fossiliferous nodules to the vertebrate fauna and surrounding sediments are not fully determined.

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Dunsinane Site was discovered in 1990 during exploration of southern Gag Plateau at Riversleigh, NW Queensland (Fig. 1A). In one area the surface was strewn with fragments of fossil bone, fossil wood and nodules of rock that contained leaves, wood, other plant material and invertebrates. Dunsinane Site is the only fossil site at Riversleigh containing plants and one of the few yielding arthropods (Archer et al., 1994). The site was also distinctive in that the fossils were associated with a soft, apparently unconsolidated sediment, rather than embedded in solid limestone. Issues to be resolved regarding this site included the nature and provenance of the fossilised plant and arthropod material, and the relationships of this material to other Riversleigh sediments.

CONCEPTS AND TERMINOLOGY

Palaeontological concepts, biostratigraphy and taxonomic classification follow Archer et al. (1994) and Creaser (1997). The terms 'Dunsinane limestone', 'Dunsinane deposit', 'Dunsinane sediment' and 'Dunsinane calcrete' are used here informally.

STRATIGRAPHY AND GEOLOGY

Representative rock types from Dunsinane Site have been examined by powder X-ray diffraction, SEM and thin-sectioning techniques. A sample of 4 nodules was used for destructive analysis. The area around Dunsinane Site is dominated by 4 main rock types: Precambrian quartz-

ite, ferruginised deposits, overlying Tertiary limestone and the Dunsinane limestone.

PRECAMBRIAN QUARTZITE

The grey Precambrian quartzite is a massive, thick tabular-bedded, crystalline pure quartz sediment. This and a laminated chert constitute the terrain around Gag Plateau and form the basement underlying the Dunsinane deposit.

FERRUGINISED DEPOSITS

Outcrops of ferruginised deposits generally do not exceed 15m in diameter. The ferruginisation is apparently related to localised groundwater activity. This type of deposit occurs throughout the Riversleigh area, particularly along geological boundaries. Around Dunsinane Site such deposits occur in the Precambrian quartzite, overlying Tertiary limestone, and at a point at the junction of the Precambrian quartzite and the Dunsinane sediment, apparently post-dating all of these sediments. In general they consist of pisolitic iron oxide, and iron oxide-enriched alterations of the sediments in which they occur.

OVERLYING TERTIARY LIMESTONES

The hard, micritic, Tertiary limestones directly overlie the Dunsinane limestone. These limestones exhibit vertical changes in colour and frequency of molluscs and calcareous mud clasts, all of which may be construed as primary bedding features. Occasional vertebrate bone fragments occur with molluscs which are very common and well-preserved. Contact of the Tertiary Limestone with the underlying Dunsinane sediment is

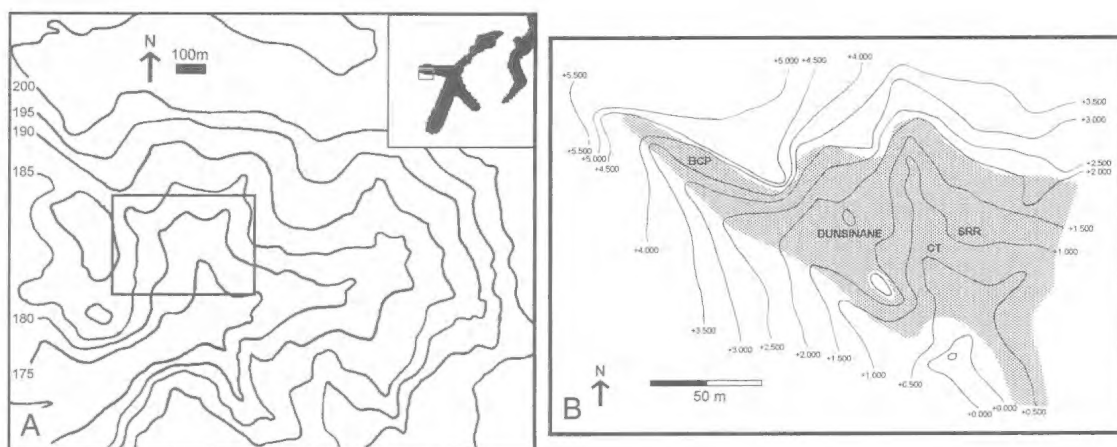


FIG. 1. A, Southern Gag Plateau and Dunsinane Site Local area map. Study area in B outlined. Contours at mAHD. (Southern Gag Plateau map inset from Megirian 1992). B, Dunsinane Site study area indicating the positions of Dunsinane, Bernie's Cooking Pot (BCP), Custard Tart (CT) and Sue's Rocky Road (SRR) Sites. Stipling=Dunsinane limestone. Contours metres from arbitrary field datum.

apparently undulatory, and may be unconformable.

DUNSINANE LIMESTONE

The Dunsinane limestone outcrop is at least 150 m across. It includes the fossil sites Bernie's Cooking Pot (BCP), Custard Tart (CT) and Sue's Rocky Road (SRR) (Fig. 1B), which have previously been regarded as separate sites.

The limestone has been severely weathered, resulting in replacement of most of the original sediment and its sedimentary structures by soft calcrete. Relict unweathered outcrops occur as sandy limestone with apparent flat bedding and minute bone fragments. Because the overlying limestone is closely associated with these relict outcrops, it appears that the weathering event post-dates the deposition and erosion of the overlying sediment.

Because the fine, well-sorted particles and apparent flat-bedding does not indicate high energy flow, the Dunsinane sediment was probably deposited in a pond or lake. This relatively arenaceous sediment was probably deposited under near shore conditions in a quartz-rich Precambrian terrain.

Fossil bones and nodules are preserved with brown iron oxide-rich fluorapatite (fluorapatite=calcium fluoride phosphate; $\text{Ca}_5(\text{PO}_4)_3\text{F}$). Energy dispersive X-Ray spectrometry demonstrated that iron oxide appears to be included within euhedral fluorapatite crystals. Fluorapatite has replaced the majority of structures within

nodule matrices. Bones are impregnated with iron-oxide rich fluorapatite, particularly around the inner parts. Bones and nodules occur in relict in situ sediment and in the surface layers across the area of the outcrop. Nodule fragments and fragments of fossil wood derived from weathered nodules are common. There are also amorphous concretions of fluorapatite and sparry calcite deep within the calcrete (1m depth) in some places.

MODEL OF POST-DEPOSITIONAL HISTORY

Weathering is a striking feature of the Dunsinane sediment. The calcrete is most likely autochthonous because of the relationship between relict unweathered outcrops of Dunsinane sediment and overlying rock. Local groundwater activity has resulted in ferruginisation in the vicinity, although this has not occurred at Dunsinane Site itself. Meteoric and surface water are the most likely agents responsible for chemical weathering of the original Dunsinane sediment.

Severity of weathering has been influenced by permeability of the original Dunsinane sediment, impermeability of the Precambrian quartzite and Tertiary limestone, the situation of Dunsinane Site at the junction of 3 drainage channels, and its position near the top of the local drainage network.

Water focussed on Dunsinane Site by the local drainage system was channelled into the permeable Dunsinane sediment before draining away

into the lower catchment. This caused the chemical weathering of the limestone responsible for: 1, apparent subsidence, slumping and surface lowering of the sediment; 2, accumulation of a surface lag of fossils mineralised with insoluble flourapatite; 3, partial dissolution and precipitation of flourapatite bodies deep in the original sediment; and 4, a thin calcareous duricrust which has cemented surface debris.

FLORA AND FAUNA

VERTEBRATES. Due to weathering and poor condition of the fossilised bone, identifiable vertebrate fossils from Dunsinane Site are relatively uncommon. However, there is marked diversity implied by the number of groups present. In contrast with many Riversleigh sites, fish and bird remains have not yet been found at Dunsinane Site. The Vertebrates includes:

- Class Reptilia
- Order Testudines
- Family Chelonidae
- genus & sp. indet.**
- Order Crocodilia
- Family Crocodylidae
- ?Baru sp.**
- Class Mammalia
- Order Marsupialia
- Suborder Diprotodontia
- Family Wynyardiidae
- ?Namilamadeta sp.**
- Family Diprotodontidae
- Subfamily Diprotodontinae
- ?Bematherium sp.**
- Subfamily Zygomaturinae
- ?Neohelos sp.**
- Family Macropodidae
- Subfamily Balbarinae
- Nambaroo sp. nov.**
- genus & sp. indet.**
- Subfamily Balungamayinae
- ?Wabularoo sp.**
- Order Placentalia
- Suborder Chiroptera
- Family Hipposideridae
- ?Brachipposideros sp.**

Neohelos, *Brachipposideros*, large crocodilians and chelonid turtles which are known from Riversleigh sediments of various Oligocene and Miocene ages are thus not useful for more precise biocorrelation. At Riversleigh wynyardiids are known only from System A and B faunas (Archer et al., 1994). Primitive balungamayine and balbarine kangaroos such as *?Wabularoo* and

Nambaroo respectively (the latter appears to be conspecific with a very primitive form from System A White Hunter Site (Cooke, 1997)), are known from Riversleigh System A and B faunas. With the exception of Pleistocene *Diprotodon optatum*, diprotodontines are restricted to System A at Riversleigh (Black, 1997). Thus we regard the fauna as most likely a System A fauna.

INVERTEBRATES

Insect fragments are often quite small, usually around 1mm and include a variety of beetle elytra and beetle prothoraces which show similarities to those of curculionids (weevils) and buprestids (jewel beetles). Curculionids have been found in the Upper Site assemblage (Archer et al., 1994), although the long history of this group makes them of little biostratigraphic use. Termite remains may also be present.

A partial gastropod shell has been identified as a probable terrestrial camaenid (W. Ponder pers. comm. 10/95). Camaenids which are known from the Mesozoic occur in System A (Archer et al., 1994) and are likely to occur in Riversleigh sediments of all ages.

FLORA

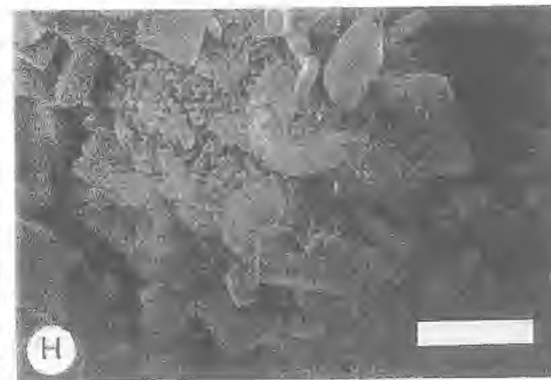
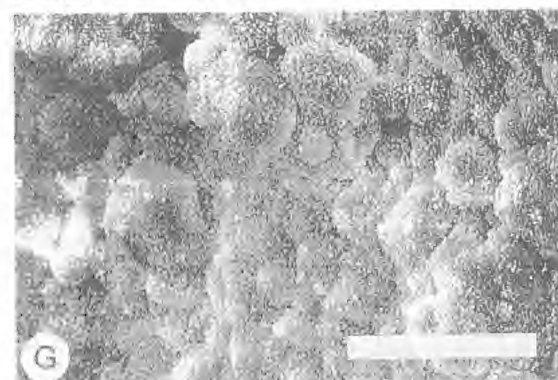
The plant assemblage consists of small pieces of twig-like wood (some stems may originally have been 3-4cm in diameter), leaves, seeds and reproductive organs.

The various types of wood imply high diversity. Angiosperm wood is present as well as probable gymnosperm wood. Leaf fragments are invariably broad and serrate-margined. Leaf cuticles are intact in a number of specimens.

There are several pneumatophore-like organs up to 2cm in diameter with a central aerenchyma of elongate cells and a narrow epidermal layer with structures resembling lenticels.

Groups recognised include Proteaceae, Casuarinaceae, Myrtaceae and possibly Epacridaceae (R. Hill pers. comm. 9/95, 10/96). Proteaceae are evergreen trees and shrubs, and are known from the Early Cretaceous to Holocene (Hill, 1994). The generally xeromorphic Casuarinaceae have a record from the Paleocene to Holocene (Hill, 1994). Myrtaceae are known from the mid-Paleocene to Holocene (Martin, 1994). The Epacridaceae which are prominent in extant scleromorphic floras have existed in Australia since the Late Cretaceous (Jordan & Hill, 1996).

Serrate leaves are not good indicators of a tropical closed forest origin (R. Hill pers. comm.



9/95). Apparent growth rings and false growth rings are evident in some wood samples. Some rings are broad, inferring a long growth season which seems to be terminated abruptly (R. Hill pers. comm. 10/95). In general the associated floristics and the timing of fossil occurrences of epacrids throughout the Tertiary coincide with temperate climatic conditions, and the nature of the macrofossil record is inconsistent with modern tropical or sub-tropical rainforest (Jordan & Hill, 1996). Pollen has been recovered from the nodules but not yet analysed.

PALAEOENVIRONMENTAL IMPLICATIONS

Biocorrelation of the Dunsinane Site fauna with that of White Hunter Site (via *Nambaroo* and *Bematherium*) allows tentative age assessment. White Hunter Site has been correlated with Etadunna Faunal Zone D (Ngama LF, Lake Palankarinna) on the ilariid, *Kuterintja ngama* (Myers & Archer, 1997). Sediments associated with this South Australian fauna have been palaeomagnetically dated at 24.7–25 Ma (Late Oligocene; Woodburne et al., 1994). This interval coincides with an 'icehouse' event, climatic conditions normally characterised by cooler, drier, seasonal climatic conditions (Frakes et al., 1987). The 'greenhouse'/'icehouse' climatic fluctuations of the Tertiary are reflected in the sedimentary and terrestrial fossil records of Australia (Frakes et al., 1987; Archer et al., 1995). The characteristics of the Dunsinane Site flora so far observed may indicate 'icehouse' conditions.

TAPHONOMY

PHOSPHATISATION OF FOSSIL ASSEMBLAGE

Early diagenetic phosphatisation, usually associated with microbial activity, has been identified as the mode of preservation of phosphatic nodules and exceptionally preserved fossils (i.e. Balson, 1980; Müller, 1985; Pinna, 1985; Seilacher et al., 1985; Soudry & Lewy, 1988; Allison,

1988a, b, c; Martill, 1988, 1989, 1990; Lucas & Prévôt, 1991; Briggs & Kear, 1993; Briggs et al., 1993). As confirmed by laboratory experiments (i.e. Prévôt & Lucas, 1986; Hirschler et al., 1990; Briggs et al., 1993; Briggs & Kear, 1993), microbially mediated phosphatisation can occur within or adjacent to bacteria, and can result in the formation of globular apatite microstructures that faithfully preserve the structure of organisms, sometimes at the microscopic level. Conditions under which fluorapatite replacement of organic tissue and carbonates may occur are (Lucas & Prévôt, 1991): 1) a concentration of organic phosphorous is required in the system (i.e. the sediment); 2) anoxic conditions which support bacteria capable of precipitating apatite; 3) acidic conditions that destabilise carbonates; these circumstances commonly occur in the interstices of phosphate-rich sediments. These conditions may be enhanced by 'closure' by a thin film of sediment or bacterial slime, or enclosing structures of organisms or sediment (i.e. carapaces, pore spaces) that contain the optimal environment for apatite precipitation (Krajewski, 1984; Seilacher et al., 1985; Martill, 1988, 1989, 1990; Soudry & Lewy, 1988; Hirschler et al., 1990; Lucas & Prévôt, 1991; Wilby & Martill 1992; Briggs et al., 1993; Briggs & Kear, 1993).

Characteristic fluorapatite microstructures very similar to those found in fossils from elsewhere in the world thought to be preserved in this way occur in nodule material examined by SEM (Fig. 2 G,H). The lack of distortion or crushing of tissues, preservation of the cellular structures of leaves (see below) and presence of organic material in the Dunsinane nodules indicate early diagenetic, pre-compaction mineralisation. This process is suggested as the mode of preservation for the 3D arthropod fossils from Upper Site (Duncan & Briggs, 1996). Fragments of algal layers in nodule material may indicate thin microbial films that 'sealed' tissues, enclosing conditions favourable to preservation and encouraging and accelerating mineralisation. The Dunsinane nodule material may have mineralised in a water

FIG. 2. A, Dunsinane Site nodules illustrating the variety of shapes and sizes. Scale bar=5cm. B, Some nodules have protusions (in this case a piece of fossil wood). Scale=20mm. C, Leaf fragment. D, QMF31306, a 3-dimensional fruit tentatively assigned to the Epacridaceae. E, Thin section of nodule, entirely phosphatised organic material. Note the undistorted arthropod with cuticle at lower-right. Plane polarised light. Scale=800µm. F, Transverse section of a leaf lamina. The vertically elongated cells are palisade cells, beneath them is intact spongy mesophyll tissue. Plane polarised light. Scale=200µm. G, SEM of nodule material showing the characteristic microstructure of early diagenetically precipitated fluorapatite replacing organic tissue. Scale=20µm. H, Globose fluorapatite microstructures. The pseudo-hexagonal crystals are fluorapatite. Scale=5µm.

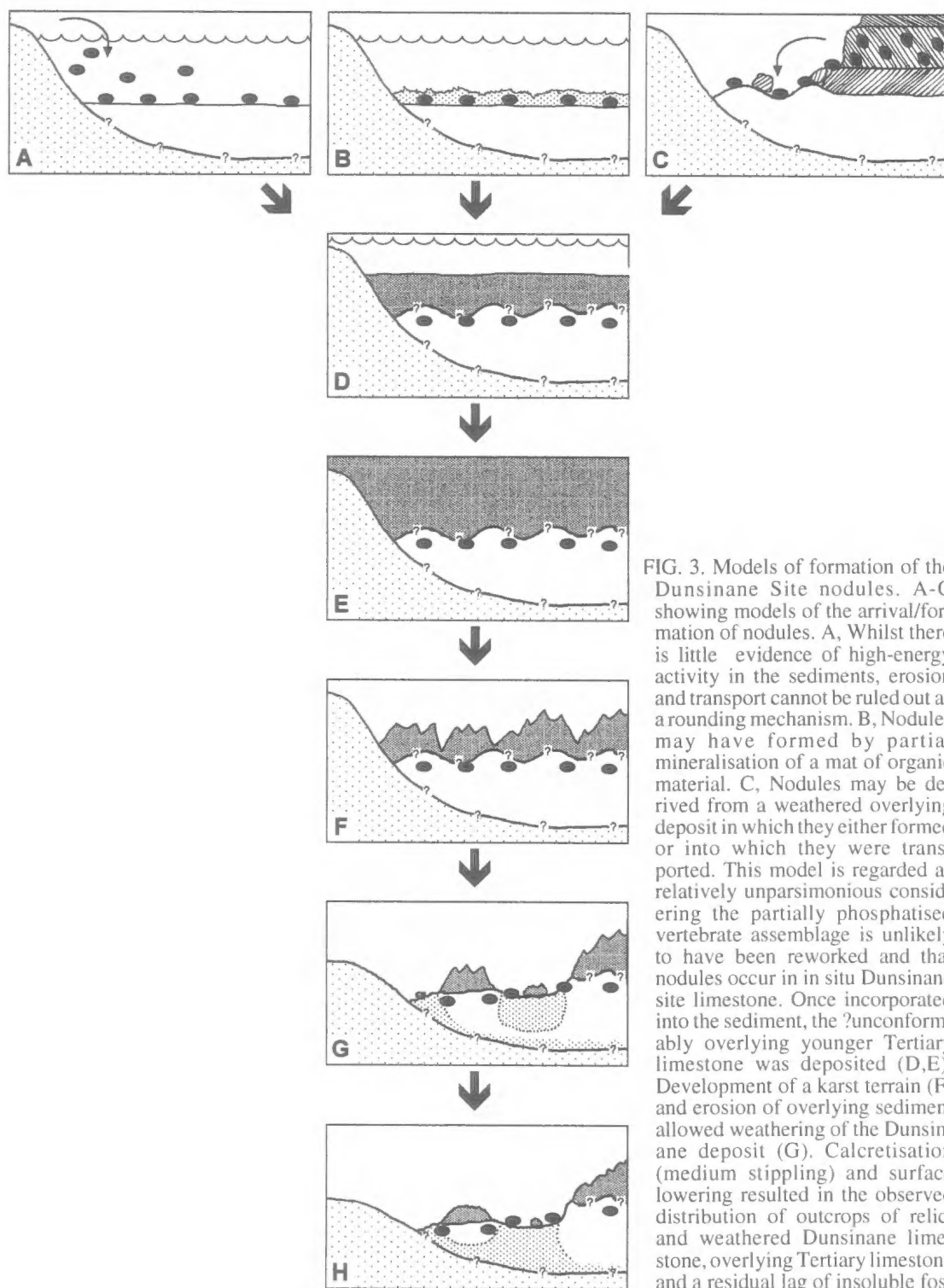


FIG. 3. Models of formation of the Dunsinane Site nodules. A-C showing models of the arrival/formation of nodules. A, Whilst there is little evidence of high-energy activity in the sediments, erosion and transport cannot be ruled out as a rounding mechanism. B, Nodules may have formed by partial mineralisation of a mat of organic material. C, Nodules may be derived from a weathered overlying deposit in which they either formed or into which they were transported. This model is regarded as relatively unparsimonious considering the partially phosphatised vertebrate assemblage is unlikely to have been reworked and that nodules occur in situ Dunsinane site limestone. Once incorporated into the sediment, the unconformably overlying younger Tertiary limestone was deposited (D,E). Development of a karst terrain (F) and erosion of overlying sediment allowed weathering of the Dunsinane deposit (G). Calcretisation (medium stippling) and surface lowering resulted in the observed distribution of outcrops of relict and weathered Dunsinane limestone, overlying Tertiary limestone and a residual lag of insoluble fossils.

body that had stagnated possibly because of a lack of freshwater input; a proximal acidic anoxic sediment such as peat or influxes of nutrients causing microbial blooms that used up available oxygen and increased available organic phosphorus. As partially decaying organic matter accumulated on and in the substrate, reducing conditions would develop leading to accumulation of iron hydroxides and destabilisation of carbonates (Allison, 1988b) and a proliferation of anaerobic microbes. Phosphatisation may have occurred in tissues in the substrate and close to it, until halted by exhaustion of available phosphate supplies, or dilution of the phosphate-rich medium perhaps by an influx of freshwater supplying oxygen and dissolved calcium carbonate.

PLANT ASSEMBLAGE

Plant organ assemblages composed of twigs, leaves and reproductive organs such as those at Dunsinane Site (Fig. 2C,D) are generally regarded as accumulations with limited lateral wind transport (Collinson, 1983; Spicer, 1980, 1989). Plant assemblages accumulated at the site of growth usually contain roots, wood fragments and plant bases; catastrophic accumulations are poorly sorted and contain components of all types (Collinson, 1983; Spicer, 1989).

Leaves most likely to be preserved in excellent condition are those that fall directly into water, since contact with the ground usually drastically reduces the chances of leaf preservation in an aquatic environment (Ferguson, 1985; Spicer, 1989, 1991). Dissolution of anti-fungal, anti-microbial and structural compounds within leaves begins immediately after immersion or contact with the ground, increasing susceptibility to microbial attack and structural collapse within 24 hours (Ferguson, 1985; Spicer, 1989, 1991). Leaf litter is generally dispersed within 50m of the parent vegetation (Ferguson, 1985; Spicer, 1989, 1991). Hill & Gibson (1986) found that the majority of leaves collected from a lake bed were from species occurring within 50m of the shore. Leaves in the Dunsinane assemblage with limited immersion damage, such as the exceptionally preserved leaf with intact cellular detail (Fig. 2F), may have been derived from vegetation that occurred within 50m of the site of preservation. Since most leaves take hours or days to sink (Ferguson, 1985; Hill & Gibson, 1986; Spicer, 1980, 1989, 1991), buoyant organs such as twigs and seeds are prevalent in the assemblage and are often in quite good condition showing little abrasion or decomposition, and the insect material is

so plentiful and diverse these factors may point to the accumulation being in shallow nearshore water.

The plant material thus appears to be part of a proximal assemblage, possibly occurring as an immersed mat of vegetation. The process of mineralisation that preserved the plant material must have occurred in the early stages of degradation since leaves have limited structural damage and intact cellular structure, in particularly spongy mesophyll tissue which is generally the most susceptible to breakdown (Spicer, 1989). The pneumatophore-like organs in the nodule assemblage could indicate anoxic conditions close to the site of preservation.

PROVENANCE AND FORMATION OF THE PHOSPHATISED NODULES

The Dunsinane Site nodules (Fig. 2A,B) may have formed in a variety of ways. Their sub-rounded shape is possibly caused by transport but this is not supported by the lack of any other evidence of high-energy flow. More lightweight fresh clods of organic material may have been sub-rounded by transport and subsequently deposited and phosphatised. However, it is debatable whether the nodule material had been subject to a sufficient compression and consolidation, given the freshness and lack of distortion of some fossil structures. The nodules may have formed at Dunsinane Site, as parts of a mat of fresh organic material resting on the sediment surface. The radiation of mineralisation from points within the mat may have produced the somewhat rounded, but otherwise variably sized and shaped nodules. Roundness of nodules may also be attributed to weathering whilst embedded in the sediment and after exposure, resulting in continuous exfoliation of outer layers.

MODELS FOR ACCUMULATION AND PROVENANCE AND FORMATION OF NODULES (Fig. 3). Allochthony of the nodules must be considered because of their peculiar mineralogy. Intraformational nodules may have formed in an overlying sediment which was weathered, resulting in the descent of sub-rounded nodules to the surface of the Dunsinane sediment and burial by younger Tertiary lacustrine sediment (hence the unconforming contact). However, this is highly unlikely considering that nodules and other fluorapatite concretions occur within *in situ* Dunsinane sediment.

The shared mineralogy of the nodules and vertebrate fossils is compelling when considering

contemporaneity. The phosphatisation process can tend to target only those tissues which have a high organic phosphorous content (Balson, 1980; Allison, 1988 a,c), suggesting that Dunsinane Site bones, which show varying degrees of phosphate enrichment, may have been subject to this process when they were fresh and still retained some organic content. This is suggested by the greater enrichment of the inner parts of bone which would have contained high concentrations of organic material. The extreme damage to the Dunsinane Site bone, but lack of evidence of reworking or trampling (particularly in the case of a partially phosphatised, extremely damaged *Bematherium* skull with dentaries articulated) may indicate damage by the highly acidic conditions in which the plant material was preserved. This would have softened and dissolved bone in the nearby substrate. Nevertheless, the evidence is ambiguous and at this stage.

CONCLUSIONS

Dunsinane Site contains a probable System A vertebrate fauna which may be tentatively dated at 24.7-25 Ma. The fossils from Dunsinane Site are preserved with iron oxide-rich fluorapatite, which appears to have precipitated as the result of early diagenetic microbially mediated phosphatisation. The Dunsinane sediment probably formed in a low-energy environment, and has been severely weathered, resulting in a lag of insoluble fossil material on the surface. Relationships of the flora and invertebrate fauna to the other components of the site are as yet unresolved.

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A NEW SPECIES OF PALORCHESTIDAE (MARSUPIALIA) FROM THE LATE
MIDDLE TO EARLY LATE MIOCENE ENCORE LOCAL FAUNA,
RIVERSLEIGH, NORTHWESTERN QUEENSLAND

KAREN BLACK

Black, K., 1997:06:30. A new species of Palorchestidae (Marsupialia) from the late middle to early late Miocene Encore Local Fauna, Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 181-185. ISSN 0079-8835.

A single palorchestid M¹ from the Encore Local Fauna, Riversleigh, northwestern Queensland is described as *Palorchestes anulus* sp. nov. In size and morphology, it is intermediate between the M¹ of middle Miocene *Propalorchestes novaculacephalus* from System C deposits, Riversleigh and the Bullock Creek Local Fauna, Northern Territory, and that of *Palorchestes painei* from the late Miocene Alcoota Local Fauna, Northern Territory. These relationships support an early late Miocene age for the Encore Local Fauna and confirm that *Propalorchestes* is the sister-group of *Palorchestes*. Consequently, the monophyly of Palorchestidae is cast further in doubt. Species of *Ngapakaldia* and *Pitikantia* may be more appropriately regarded as plesiomorphic members of Diprotodontidae.

□ Palorchestidae, *Palorchestes*, *Propalorchestes*, late Miocene, Riversleigh.

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A recently discovered upper molar from Encore Site on the Gag Plateau, Riversleigh has increased the late Oligocene to late middle Miocene material of Palorchestinae to 9 specimens. This paucity of material, which prior to 1986 consisted exclusively of the highly derived *Palorchestes*, has made resolution of relationships within the family difficult. Although *Palorchestes anulus* sp. nov. is only known from an isolated M¹, it adds substantially to phylogenetic understanding within the family.

On the basis of vertebrate stage-of-evolution biostratigraphy the Encore Local Fauna is currently regarded as late middle to early late Miocene (approximately 10Ma; Archer et al., 1995). Taxa from Encore Site are more derived than those characteristic of Riversleigh's upper System C assemblages yet plesiomorphic relative to related taxa of the late Miocene Alcoota Local Fauna, Northern Territory (Archer et al., 1995). The species described below supports an early late Miocene age.

Institutional abbreviations used here are as follows: QMF, Queensland Museum palaeontological collection; CPC, Commonwealth Palaeontological Collection at the Australian Geological Survey Organisation, Canberra; NTMP, Art Gallery and Museum of the Northern Territory palaeontological collection; SAMP, South Australian Museum; UCMP, University of California, Berkeley. Cusp nomenclature follows Archer (1984) and Rich et al. (1978) except that their hypocone of upper molars is the metaconule

following Tedford & Woodburne (1987). Molar number homology follows Luckett (1993). Higher level systematic nomenclature follows Aplin & Archer (1987).

SYSTEMATIC PALAEOLOGY

- Order DIPROTODONTIA Owen, 1866
- Suborder VOMBATIFORMES Woodburne, 1984
- Infraorder VOMBATOMORPHIA Aplin & Archer, 1987
- Superfamily DIPROTODONTOIDEA Archer & Bartholomai, 1978
- Family PALORCHESTIDAE Tate, 1948 emend. Archer & Bartholomai, 1978

Palorchestes Owen, 1873

TYPE SPECIES. *Palorchestes azeai* Owen, 1873.

OTHER SPECIES. *P. parvus* De Vis, 1895; *P. pamei* Woodburne, 1967; *P. selestiae* Mackness, 1995.

Palorchestes anulus sp. nov.
(Figs 1-2, Table 1)

MATERIAL. Holotype, QMF30792, a right M¹ missing the posterior cingulum and anterior and posterior roots from the late middle Miocene to early late Miocene Encore Local Fauna, on the Gag Plateau, Riversleigh.

ETYMOLOGY. Latin *anulus*, link; refers to its being a structural link between *Propalorchestes* and *Pal-*

TABLE 1. Measurements (mm) of palorchestid M¹..

Species	No.	Length	Anterior width	Posterior width
<i>Palorchestes anulus</i>	QMF30792	17.1	13.5	13.0
<i>Pr. ponticus</i>	NTM P895-1	14.3	11.5	10.9
	QMF30883	15.3	-	-
	QMF30884	16.2	12.6	11.6
	QMF26612	15.2	-	10.8
<i>Pr. novae-culacephalus</i>	NTMP862-27	16.8	13.2	12.0
<i>P. selestinae</i>	QMF12455	22.6	16.6	16.9
<i>P. painei</i>	UCMP 70553 R	16.5	13.6	13.8
	UCMP 70553 L	16.8	14.4	13.7
	UCMP 70550	16.7	13.9	13.7
	UCMP 66521	17.8	14.0	13.2
	CPC6752	18.2	14.3	-
<i>P. parvus</i>	QMF 784	20.7	15.7	15.4
	QMF12476	-	15.4	15.3
	QMF2963	19.5	14.9	14.4
	QMF3719	19.3	15.0	14.2
	QMF2967	19.4	15.6	15.6
	QMF2965	20.9	-	14.5
<i>P. azael</i>	QMF772	26.6	21.9	21.5
	QMF3537	25.8	20.7	19.7
	P31370	23.3	21.8	21.1
	P31371	23.3	22.6	21.9
	P31372	26.1	22.9	21.9

orchestes and to the distinct midlink, a character of *Palorchestes*.

COMPARISON. *Palorchestes anulus* differs from *P. painei* in being proportionately narrower anteriorly and posteriorly, in its poorly developed lingual cingulum, more open transverse median valley lingually, less tightly V-shaped transverse median valley in lingual view and less well-developed hindlink.

Palorchestes anulus differs from *P. parvus*, *P. selestinae* and *P. azael* in being smaller; in having generally less well-developed links; in having a shallower, more open transverse median valley; in having a more buccally positioned midlink; in having a less well-developed, lower, less buccally extensive (i.e. in lacking the anterobuccal cingulum) anterior cingulum (compared with the high, loph-like anterior cingulum in both *P. parvus* and *P. azael*) and consequently, in lacking the deep valleys formed between the anterior cingulum and the anterior base of the protoloph.

Palorchestes anulus differs from both *P.*

parvus and *P. azael*: in lacking the second medial forelink; in having a less well-developed midlink which is deeply V-shaped, its respective anterior and posterior crests meeting lower in the transverse median valley (and more buccally) than the well-developed structure in both *P. parvus* and *P. azael*; in lacking the second buccal midlink, and having only a poorly-developed accessory crest extending anteriorly from a medial point on the metaloph; in having a poorly-developed lingual cingulum; in lacking a buccal cingulum; and in having well-developed postparaconal and postmetaconal crests extending posteriorly from the apices of the paracone and metacone respectively.

Palorchestes anulus differs from *P. selestinae*: in having a short crescentic lingual cingulum; in lacking the anterolingual forelink; in lacking the secondary midlink and the minor lingual midlink; and in having less-crenulated enamel at the base of the protoloph and metaloph.

Palorchestes anulus differs from *P. parvus* in having a straighter, less crescentic metaloph and in having a less crenulate transverse median valley.

Palorchestes anulus differs from *P. azael* in lacking the well-developed lingual midlink; in having a better-developed posterior cingulum; and in having a hindlink developed.

DESCRIPTION. Tooth rectangular, bilophodont, consisting of an anterior protoloph connecting the protocone with the paracone, and a posterior metaloph connecting the metacone with the metaconule. Protoloph anteriorly convex; metaloph slightly more linear, with its lingual end deflected posteriorly. Metaconule highest cusp; the paracone and protocone subequal in height; metacone lowest cusp (taking into account slight wear on the apices of the major cusps). Anterior cingulum well-defined but low on the anterior base of the crown, extending lingually from the anterobuccal tooth margin to the anterolingual base of the protocone. Lingual cingulum short, poorly defined, connecting the posterolingual base of the protocone to the anterolingual base of the metaconule. Posterior cingulum not preserved (but suggested by the short crest at the posterolingual base of the metaconule).

Forelink well-developed, extending anteriorly

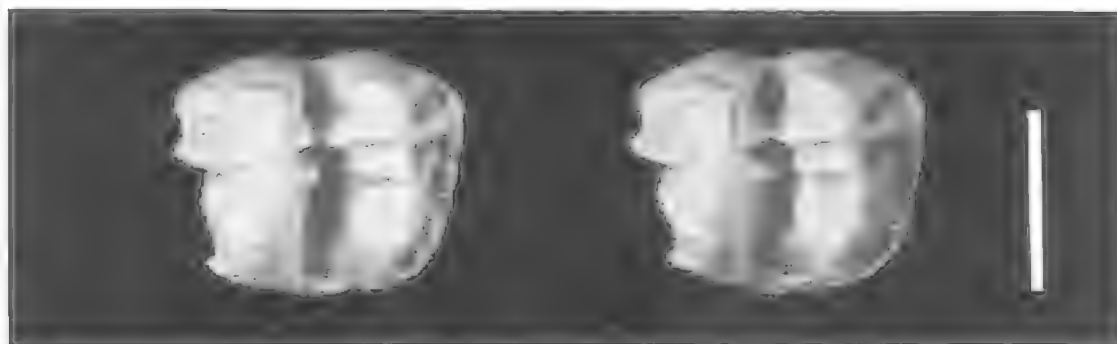


FIG. 1. *Palorchestes anulus* sp. nov. Holotype, QME30792: Occlusal stereopair of right M¹. Bar indicates 10 mm.

from the apex of the protocone at a point slightly lingual to the paracone apex, meeting the anterior cingulum at the parastylar corner of tooth. Two accessory crests (or incipient links) poorly-defined: one originating at the paracone and fading down the anterobuccal face of the crown; the second originating from the protocone at a point slightly lingual to the main forelink, extending anteriorly and slightly buccally, along the longitudinal axis of the tooth, terminating in the valley between the anterior base of the protocone and the anterior cingulum. Single midlink formed by the junction of respective anterior and posterior crests from the metaloph and protocone meeting low in the transverse median valley (making the link sharply V-shaped in lateral view) approximately 4 mm from the buccal tooth margin. An additional moderately-developed crest extending anteriorly from the apex of the metaloph into the transverse median valley but without a connecting crest from the protocone. Hindlink well-developed, extending posteriorly and slightly lingually from the metaloph, approximately 5 mm lingual to the buccal tooth margin. A thickening in the enamel (the posterior metacone buttress) posterior to the metacone apex but probably not developed into a crest. A similar buttress on the posterior flank of the protocone.

DISCUSSION. Palorchestids are rare, fragmentary components of Tertiary fossil assemblages. Until recently, the family consisted of only the primitive, generalised, late Oligocene *Ngapakaldia* and *Pitikantia*, and the derived, highly specialised late Miocene to late Pleistocene *Palorchestes*. The large temporal and morphological gaps separating these groups has made relationships within the family difficult to resolve. Stirton (1967) recognised 4 subfamilies within the Diprotodontidae and included *Ngapakaldia* and

Pitikantia in the Palorchestinae (later raised to family status) based on similarities in basicranial morphology to *Palorchestes*. However, these supposed apomorphies are also shared with the Diprotodontinae and have since (e.g. Archer 1984) been interpreted as symplesiomorphic within Vombatomorpha. Consequently, Archer (1984) concluded the Palorchestidae was not monophyletic, a view later confirmed by Murray (1986; 1990), with his description of *Propalorchestes* dentitions and cranial fragments from the middle Miocene Bullock Creek Local Fauna, Northern Territory, and several Oligo-Miocene sites at Riversleigh, Murray (1990) concluded that *Propalorchestes* is the plesiomorphic sister-taxon of *Palorchestes* and demonstrated a structural transition from the selenodont wynyardiid molar pattern to the bilophodont palorchestid molar pattern. He further concluded that *Ngapakaldia* and *Pitikantia*, having suppressed their selenodont heritage, show closer affinities to the fully bilophodont diprotodontids than palorchestids. Preliminary analyses of late Oligocene and Miocene diprotodontids and palorchestids from Riversleigh further suggest that *Ngapakaldia* and *Pitikantia* should be regarded as primitive members of Diprotodontidae.

Palorchestes anulus supports a *Propalorchestes*/*Palorchestes* sister-group relationship and confirms doubts (Archer & Bartholomai, 1978; Archer, 1984; Murray, 1990; Mackness, 1995) about the monophyly of the family. The M¹ of *P. anulus* is intermediate in a number of key features between the middle Miocene *Propalorchestes novaculacephalus* from the Bullock Creek Local Fauna, and System C deposits at Riversleigh, and *Palorchestes painei* from the late Miocene Alcoota Local Fauna. The Encore M¹ consistently groups with *Propalorchestes novaculacephalus* and *P. painei* falling within the

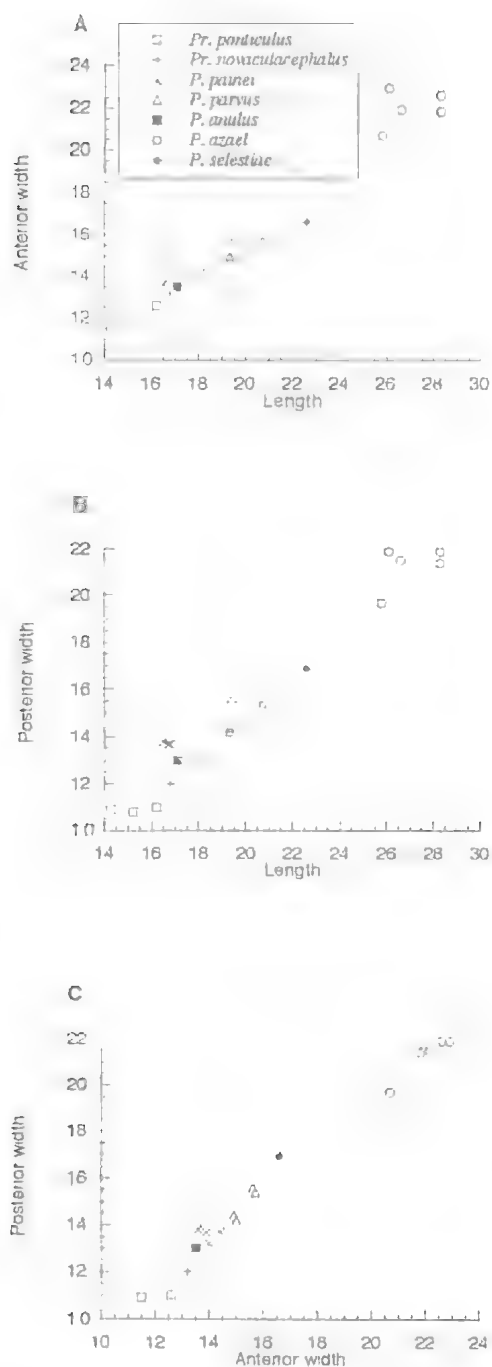


FIG. 2. Bivariate plots of M¹ tooth dimensions for species of *Palorchestes* and *Propalorchestes*; A, length against anterior width; B, length against posterior width; C, anterior width against posterior width. Scale in mm.

size range of both species (Fig. 2A-B). Proportionally (Fig. 2C), however, *P. anulus* groups more closely with *P. painei*. Along the *Propalorchestes*-*Palorchestes* morphocline (Fig. 2C) there is a noticeable shift towards a squaring-up of the molar crown. *Propalorchestes* molars are more elongate than wide, and trapezoidal in occlusal view, a feature most obvious in the molars of the plesiomorphic *Pr. ponticulus*. In contrast, the posterior width of the M¹ of the highly derived *P. azael*, is similar to its anterior width, giving the tooth a more rectangular profile in occlusal view. The initial stages of this transition are evident within *P. anulus*. The metaloph of M¹ is less convex than in *Propalorchestes* and approaches the length of the protoloph, thus increasing the posterior width of the molar crown. This feature is reflected in the position of *P. anulus* on the morphocline (Fig. 2C) and is indicative of its derived state relative to *Propalorchestes*.

Other features of the M¹ that indicate *P. anulus* is derived with respect to *Propalorchestes* include its well-developed forelink and accessory forelink and well-developed hindlink; a higher, stronger midlink; a more open transverse median valley; well-developed convex posterobuccal postparaconal and postmetaconal crests; well-developed buttresses on the posterolingual face of the protocone and metacone; a less convex metaloph; and a well-developed parastyle connected to the protoloph by the forelink. Mackness (1995) listed the well-developed midlink on M¹ as the single synapomorphy of *Palorchestes* as opposed to *Propalorchestes*. The Encore species, with a strong, high midlink, is included in *Palorchestes* as a primitive member of the genus, rather than as a derived species of *Propalorchestes*.

The Encore deposit is regarded to be most probably early late Miocene in age (Archer et al., 1995). Stage-of-evolution biocorrelation of marsupial taxa including vombatids (Krikmann (pers. comm.), propleopine kangaroos (Wroe, 1996), koalas (Archer et al., 1995), dasyurids (Wroe, this volume) and thylacoleonids (Gillespie, this volume) suggest the Encore Local Fauna lies somewhere between Riversleigh's upper System C assemblages and the late Miocene Alcoota Local Fauna and is probably around 10 Ma. The presence of *P. anulus* at Encore Site, structurally intermediate between the middle Miocene *Pr. novaculacephalus* and the late Miocene *P. painei*, further substantiates an early late Miocene age.

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DIVERSITY AND BIOSTRATIGRAPHY OF THE DIPROTODONTOIDEA OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

KAREN BLACK

Black, K. 1997:06:30: Diversity and biostratigraphy of the Diprotodontoidea of Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 187-192. Brisbane. ISSN 0079-8835.

The diversity and distribution of Riversleigh's Diprotodontoidea is discussed with respect to current understanding of the local stratigraphic sequence. The more plesiomorphic diprotodontid and palorchestid taxa are restricted to the older System A Local Faunas. *Neohelos* and *Propalorchestes* range throughout Systems A, B and C exhibiting a morphocline. Stage-of-evolution biocorrelation with other Australian and New Guinean Tertiary mammal faunas is in accord with previously established biostratigraphic hypotheses. However some basal Riversleigh deposits may predate the central Australian Wipajiri and Etadunna Formations. Diprotodontoid diversity is high in System A deposits, low in System B and relatively high in System C. Abundance is high in System C deposits and low in Systems A and B. Only two taxa extend into the Pleistocene. Patterns of diversity and abundance are discussed in view of Australia's changing Cainozoic climate. □*Diprotodontidae*, *Palorchestidae*, *Riversleigh*, *Tertiary*.

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The paucity of radiometrically dated Australian Tertiary freshwater fossil deposits has resulted in marsupial stage-of-evolution biochronology being the most commonly employed method of dating fossil assemblages (Woodburne et al., 1985). Fundamental to this method is an adequate understanding of phyletic succession within the taxon (Megirian, 1994). Chronologic and phyletic succession within diprotodontoid lineages are well documented (e.g. Stirton et al., 1967; Murray, 1990b; Murray et al., 1993). Consequently, the group has played a major role in previous biochronologic analyses (e.g. Stirton et al., 1967; Woodburne et al., 1985; Woodburne et al., 1993; Archer et al., 1994; Archer et al., 1995) and has contributed significantly to the construction of the chronological framework of Australia's Tertiary mammal faunas.

Similarly, because of limited stratigraphic data and the lack of radiometric dates, much of the current chronologic sequence of Riversleigh's local faunas has been constructed on the basis of vertebrate biocorrelation (Archer et al., 1989). Recent reappraisal of diprotodontoid material from Riversleigh indicates at least 9 genera and 18 species. This paper outlines the diversity and distribution of diprotodontoids throughout the Riversleigh Systems and discusses their bearing on current biostratigraphic understanding. Biocorrelation of Riversleigh's Oligocene-Miocene deposits with other Australian fossil assemblages is also discussed.

Lithostratigraphy and Systems terminology follow Archer et al. (1989, 1994a). Cusp nomenclature follows Archer (1984) and Rich et al. (1978). Molar homology is that proposed by Lockett (1993). Premolar number follows Flower (1867). Higher level systematic nomenclature follows Aplin & Archer (1987).

BIOSTRATIGRAPHY

Figure 1 lists the diprotodontids and palorchestids from different local faunas within Riversleigh's stratigraphic units. These units are defined by Archer et al. (1989, 1994a): System A, late Oligocene to early Miocene; System B, early to middle Miocene; System C, middle to early late Miocene; and Pleistocene assemblages.

Silvabestius michaelhirti is the most plesiomorphic zygomaturine recognised (with the possible exception of *Raemotherium yatkolai* Rich et al., 1978) and may be antecedent to the entire zygomaturine radiation (Black & Archer, 1997a). Four species of *Neohelos* are recognised (P. Murray pers. comm.). *Neohelos* sp. nov. 1, a small plesiomorphic form; *N. tirarensis* a medium-sized moderately derived form from the Kutjamarpu Local Fauna, South Australia; *Neohelos* sp. nov. 2, a large derived form from the Bullock Creek Local Fauna, NT, antecedent to *Kolopsis torus* (Woodburne, 1967) of the late Miocene Alcoota Local Fauna, NT; and *Neohelos* sp. nov. 3, a highly derived form structurally

	SYSTEM A										SYSTEM B						SYSTEM C										PL EI
	L	MID					H	LOW	MID	HIGH	C+																
LOCAL FAUNAS	D	B	H	B	S	J	V	A	W	W	C	N	D	M	I	R	G	D	J	H	J	90	J	D	C	E	T
<i>S. michaelbirti</i>			1																								
<i>S. johnnilandi</i>							2																				
<i>Silvabestius</i> sp.	1																								10		
<i>Neohelos</i> sp. nov. 1	1	1		1	1																						
<i>N. tirarensis</i>	1			1						1	1	1		1	1				1								
<i>Neohelos</i> sp. nov. 2																	1			4							
<i>Neohelos</i> sp. nov. 3																					2						
<i>Ni. lavarackorum</i>																1	1	1				24	1	2			
<i>Nimbador</i> sp.																					1						
Zygomaturine gen. nov.												2															
<i>B. angulatum</i>	1	1	2		4	1			3																		
<i>Bematherium</i> sp.								1																			
<i>Ngapakaldia</i> sp.					1																						
<i>Pr. ponticulus</i>	1			1	2	1				1	1	1					1										
<i>Pr. novacula cephalus</i>																			1	1							
<i>Palorchestes anulus</i>																										1	
<i>P. azael</i>																											1
<i>Diprotodon optatum</i>																											1
TOTAL	5	2	2	3	4	2	1	1	1	2	2	2	1	1	1	1	3	1	2	2	1	2	1	1	1	1	2

FIG. 1. The distribution of diprotodontoid taxa through the Riversleigh sequence. Numbers indicate the minimum number of individuals for each species found in a given local fauna. PLEI=Pleistocene. System B heading is subdivided into: L=Low, MID=Middle and H=HighLocal Fauna Abbreviations: AL, Alsie; 90, Alan's Ledge 1990; BO, Burnt Offering; BR, Bone Reef; CO, Cleft of Ages (tentatively regarded as System C); CS, Camel Sputum; D, D-Site; DI, Diprotodont Site; DS, Dome Site; DT, Dirk's Towers; EN, Encore Site; G, Gag Site; H, Hiatus Site; HH, Henk's Hollow; IN, Inabeyance; JA, Jeanette's Amphitheatre; JC, Jim's Carousel; JJ, Jaw Junction; JJS, Jim's Jaw Site; MM, Mike's Menagerie; NG, Neville's Garden; RT, Ringtail Site; SB, Sticky Beak Site; TE, Terrace Site; WH, White Hunter; VIP, VIP Site; WW, Wayne's Wok.

transitional between *Neohelos* sp. nov. 2 and *Kolopsis yperus* (Murray et al, 1993) from the late Miocene Ongeva Local Fauna, Waite Formation. *Bematherium* sp. is known from a single maxillary fragment which is plesiomorphic relative to *B. angulum*. A new unnamed species of *Ngapakaldia* is more derived than the central Australian *N. tedfordi* but plesiomorphic relative to *N. bonythoni*. Fragmentary material of Zygomaturine gen. nov. has an uncertain phylogenetic position. *Nimbador* sp. is similar to *N. lavarackorum* in size, molar morphology and cranial profile; however, differences in upper premolar morphology may imply a more plesiomorphic position within the genus. However, I doubt whether this single skull is indicative of a new species. Extreme intraspecific variation in P³ morphology is common among Tertiary zygomaturines (e.g. *Neohelos* spp.; P.

Murray pers. comm.) with reduction or loss of premolar cusps a relatively common phenomenon. Comparable cranial material for *Ni. lavarackorum* has yet to be processed. *Propalorchestes ponticulus* (Murray, 1990b) is plesiomorphic relative to *P. novaculacephalus*. *Propalorchestes novaculacephalus* occurs in the Bullock Creek Local Fauna; Murray (1990b) indicated that this material is more derived than the Riversleigh specimens. *Palorchestes anulus* is intermediate between *Pr. novaculacephalus* and *Palorchestes painei* from the late Miocene Alcolota Local Fauna (Black, 1997). *Palorchestes azael* and *Diprotodon optatum*, the most derived members of Palorchestidae and Diprotodontidae, respectively, are known from Terrace Site, which has been radiocarbon dated at approximately 23,900±4,100-2,700 years BP (Davis & Archer, 1997).

DISCUSSION

AGREEMENT WITH PROPOSED STRATIGRAPHY. The distribution of diprotodontoids throughout the Riversleigh systems is generally consistent with Archer et al.'s (1989, 1994a, 1995) proposed stratigraphic framework. The most plesiomorphic forms are restricted to the older System A local faunas, and more derived taxa become more abundant in Systems B and C.

A similar pattern of distribution is evident within lineages. There is a gradual evolution in cranial and dental morphology accompanied by an increase in body size within *Neohelos* and *Propalorchestes*, respectively, through the Riversleigh sequence (Murray, 1990b; pers. comm.). Although some temporal overlap is evident, generally *Neohelos* sp. nov. 1 is the dominant form in System A, *N. tirarensis* is most abundant in System B, *Neohelos* sp. nov. 2 spans low to high System C and *Neohelos* sp. nov. 3 is unique to high System C Jaw Junction Site.

A similar succession is exhibited by palorchestids. Plesiomorphic *Propalorchestes ponticulus* is relatively common in System A and B Sites, and is succeeded by the more derived *Pr. novaculacephalus* in mid-high System C Sites.

INTRACONTINENTAL COMPARISONS. The Riversleigh assemblages contain the most diverse array of diprotodontids and palorchestids of any single region on the continent. Of the 9 genera, *Neohelos*, *Nimbador*, *Ngapakaldia*, *Propalorchestes* and *Palorchestes* are also known from the Oligocene-Miocene in central and northern Australia. The biochronological potential of some of these genera is, however, limited, because of uncertainty about interspecific affinities. *Neohelos*, *Propalorchestes* and *Palorchestes*, are biochronologically most significant.

Neohelos tirarensis from System B is close to the type material from the Kutjamarpu Local Fauna suggesting age equivalence; this is supported by other shared taxa such as *Wakiewakie lawsoni* (Godthelp et al., 1989), *Paljara* (Archer, 1994), *Wakaleo oldfieldi* (A. Gillespie pers. comm.), *Namilamadeta*; *Nambaroo* (Archer et al., 1989) and *Litokoala* (Black & Archer, 1997b).

Neohelos sp. nov. 1 in Systems A-C is more plesiomorphic than *N. tirarensis* suggesting that some of Riversleigh's stratigraphic units predate the Kutjamarpu Local Fauna. *Neohelos* from faunal zones D-E of the Etadunna Formation have not been specifically identified (Woodburne et

al., 1993). Murray (pers. comm.) suggests that if this material is found to represent *tirarensis* then some of Riversleigh's older deposits may predate mammal-bearing Etadunna Formation.

Myers & Archer (1997) correlated White Hunter Site (System A) and Mammalon Hill (Zone D, Etadunna Formation), the latter 24.7-25 MY BP (Woodburne et al., 1993).

?*Ngapakaldia* sp. nov. in System A extends the generic distribution from South Australia. This species appears to be more derived than *N. tedfordi* from the Ngapakaldi and Ngama Local Faunas (Etadunna Fmn) and the Tarkarooloo Local Fauna (Namba Fmn), yet plesiomorphic relative to *N. bonythoni* from the Ngapakaldi Local Fauna. *Ngapakaldia* also occurs in faunal zones C, D and E of the Etadunna Fmn. As with *Neohelos*, species level identification is necessary before *Ngapakaldia* will be of use in biocorrelation.

Propalorchestes novaculacephalus and *Neohelos* sp. nov. 2 in low to mid System C assemblages confirms previous hypotheses (Archer et al., 1989; 1994a; 1995) that they are of a similar age to the Bullock Creek Local Fauna (Fig. 2). Correlation is further supported by the shared *Nimbacinus dicksoni* (Muirhead & Archer, 1990), *Wakaleo vanderleuri* (Murray & Megirian, 1990) and *Balbaroo* sp. (Flannery et al., 1983).

Neohelos sp. nov. 3, the largest and most derived species of *Neohelos*, occurs in the Jaw Junction assemblage suggesting that this high System C deposit is younger than the Bullock Creek Local Fauna. *Neohelos* sp. nov. 3 exhibits an upper third premolar morphology that anticipates the condition found in the more derived zygomaturine *Kolopsis*, which first appears in the Alcoota and Ongeva Local Faunas of the Waite Fmn, Northern Territory. Ancestor-descendent relationships are well supported for the *Neohelos/Kolopsis/Zygomaturus* clade (Stirton et al., 1967; Murray et al., 1993). The presence of *Neohelos* material, structurally transitional between Bullock Creek's *N.* sp. nov. 2 and the Waite Formation's *Kolopsis* further suggests this correlation making some of Riversleigh's high System C deposits, such as Jaw Junction Site, younger than the Bullock Creek Local Fauna but older than late Miocene deposits of the Waite Formation.

This is also true of Riversleigh's Encore assemblage which, on the basis of its derived and often unique fauna, is believed to be early late Miocene in age (Archer et al., 1995). This is based on the

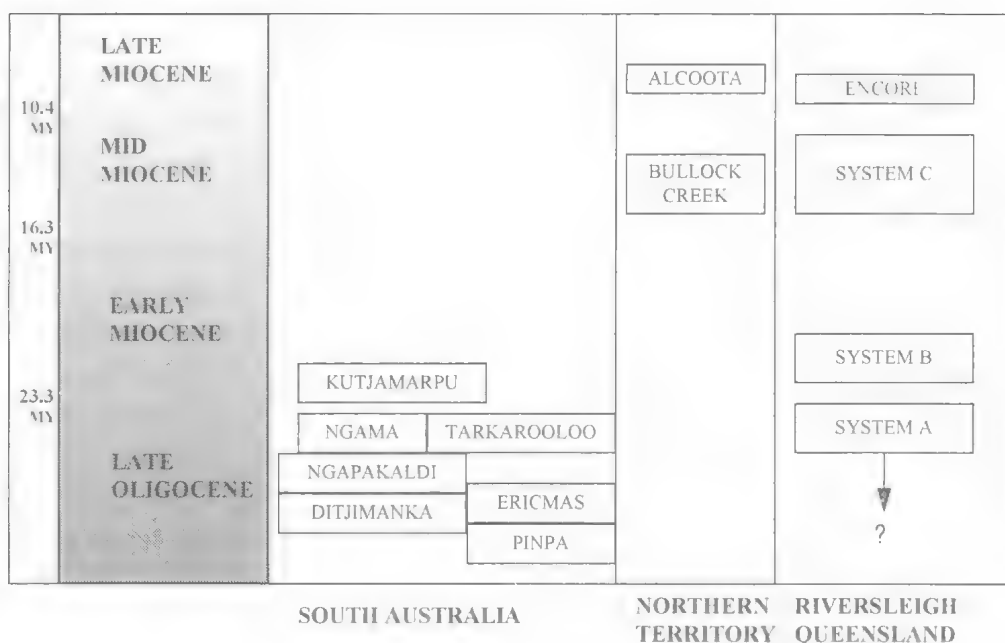


Fig. 2. Tentative correlation of Riversleigh's Oligo-Miocene fossil deposits with the Etadunna and Wipajiri Formations, South Australia and the Alcoota and Bullock Creek local faunas, Northern Territory based on diprotodontoid stage-of-evolution comparisons.

presence of several taxa which exhibit adaptations to the onset of drier climates during the late Miocene as well as taxa whose lineages extend into Pliocene and Pleistocene times. These include: *Palorchestes anulus* which is structurally antecedent to *P. painei* from the late Miocene Alcoota Local Fauna (Black, 1997); a small *Phascolarctos*; a hypselodont vombatid related to the late Cainozoic *Warendja wakefieldi* (Archer et al., 1995); a thylacoleonid intermediate between *Wakaleo vanderleuri* and the late Miocene *Wakaleo alcootense* (A. Gillespie pers. comm.); a giant rat kangaroo, *Ekaltadeta jamiemulvanei* (Wroe, 1996), which is possibly antecedent to Pleistocene *Propleopus*; and *Mayigriphus orbus* (Wroe, 1997), a dasyuromorphian with some features correlated with drier environments in modern dasyurids.

DIVERSITY AND FAUNAL CHANGE. System A sites contain the highest number of contemporaneous diprotodontoids with 5 species at Site D and 4 at Sticky Beak Site (Figs 1-2). A drop in diversity is evident in System B with only 1 or 2 species per site. Diversity increases slightly in low to middle System C assemblages with generally 1-2 contemporaneous diprotodontoid spe-

cies. Conversely, upper System C deposits exhibit a decline in diprotodontoid diversity. If we consider the small number of taxa being analysed such changes in diprotodontoid diversity may not be significant. However, a similar decline in both family- and generic-level diversity is evident in a number of other marsupial groups during the middle to late Miocene. This decline may be related to the late Miocene onset of 'icehouse' climatic conditions resulting in the regional collapse of rainforest and subsequent spread of open forest and woodland/savanna (Archer et al., 1994b; 1995).

Replacement of rainforest habitat by more open forest may have benefited select diprotodontoids which is reflected in an increase in species abundance for some System C Local Faunas. Relatively high 'minimum number of individuals' estimates for species of *Nimbadon* and *Neohelos* sp. nov. 1 have been recorded from AL90 and Cleft of Ages Sites respectively. This may suggest that individuals of these species were roaming in mobs, a feature characteristic of slow moving medium- to large-sized herbivores in relatively open environments.

It is also feasible that high abundance in the above System C assemblages, and conversely low

abundance in System A-B assemblages, may represent sampling or taphonomic biases. Likewise, the absence of diprotodontines in System B and C may be an artefact of incorrect taxonomic assignment. Even so, several zygomatic species recovered from System B and System C assemblages appear to have developed a number of diprotodontine-like features of their dentition. These include the reduction of the parastyle and loss of the hypocone on P^3 and a reduced paracristid on M_1 . A similar phenomenon has occurred in the Alcoota Local Fauna where dental and cranial morphology of the zygomatic *Alkwertatherium webbi* is convergent on that of the diprotodontine *Pyramios alcootense* (Murray, 1990a). In general, zygomatics display a higher diversity and abundance in Tertiary fossil assemblages than diprotodontines. This may reflect their greater ability to adapt to changing environments than their diprotodontine counterparts. It is further reflected in Riversleigh's System B and System C Local Faunas, where diversifying zygomatics have subsequently radiated into vacant niches occupied by diprotodontines during the late Oligocene.

Diprotodontoids are not known from Riversleigh's Pliocene assemblages. They seem to have declined markedly in generic diversity throughout the Australian Pliocene. Significant faunal turnover is characteristic of most marsupial families during the late Miocene and early Pliocene (Archer et al., 1995).

The drop in diversity of diprotodontid and palorchestid species continues into the Pleistocene, with only one member of each family represented (Fig. 1). Both species are common throughout Australia's Quaternary fossil deposits, yet both are the last of their respective lineages. This decline in diprotodontoid diversity may be a consequence of unsuccessful competition with rapidly diversifying mesic and xeric macropodoids (Archer et al., 1994).

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SILVABESTIUS GEN. NOV., A PRIMITIVE ZYGOMATURINE (MARSUPIALIA, DIPROTODONTIDAE) FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

K. BLACK AND M. ARCHER

Black, K. & Archer, M., 1997:06:30. *Silvabestius* gen. nov. a primitive zygomaturine (Marsupialia, Diprotodontidae) from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 193-208. Brisbane. ISSN 0079-8835.

A new genus and two new species of primitive Oligo-Miocene zygomaturines are described from Riversleigh, northwestern Queensland. A maxillary fragment described by Tedford as palorchestine (Marsupialia: Palorchestidae) is referred to *Silvabestius*, and is intermediate between *S. michaelbirti* sp. nov. and *S. johnnilandi* sp. nov. Trends in premolar morphology within the genus support Stirton et al.'s proposal that zygomaturines arose from primitive diprotodontine-like forms in which the parastyle on P³ was less developed. The tricuspid P³ of *S. michaelbirti* is intermediate between the bicuspid P³ of primitive diprotodontines and the more typical quadricuspid P³ of *S. johnnilandi*. Cladistic analysis of the Zygomaturinae, based largely on the upper third premolar, is compared with previous analyses.

□ *Zygomaturinae, Silvabestius, Riversleigh, Oligocene, Miocene.*

Karen Black & Michael Archer, School of Biological Science, University of New South Wales, New South Wales 2052, Australia; 4 November 1996.

Tedford (1967) described Palorchestinae gen. and sp. indet., a right maxillary fragment containing P³-M¹ and the anterior half of M² from Site D, Riversleigh, northwestern Queensland. This assignment was based on plesiomorphic features that were at the time otherwise only known in primitive palorchestids such as *Ngapakaldia* and *Pitikantia*. Tedford (1967) did, however, note enlargement of the parastylar region, a low parastyle and a more extensive posterolingual cingular shelf in P³ that appeared to anticipate development of the quadricuspid premolars of primitive zygomaturines. These features were also noted by Hand et al. (1993b) who, in light of primitive zygomaturines from northern Australia (*Nimbadon* Hand et al., 1993a; *Alkwertatherium* Murray, 1990b), Hand et al. (1993b), referred the D-site specimen to the Zygomaturinae.

Two perfectly preserved crania of the primitive zygomaturine diprotodontid, *Silvabestius johnnilandi* sp. nov. were collected at VIP Site in 1989 and a complete skull of *Silvabestius michaelbirti* sp. nov. was recovered from Hiatus Site in 1992. Both species show striking similarities in dental morphology to Tedford's Site D maxillary fragment.

This paper describes these new species and provides a phylogenetic analysis of the Zygomaturinae based on dental features. Particular attention focuses on P³, which tooth appears most useful in diprotodontoid phylogenetic analyses (Stirton et al., 1967).

Material is deposited in the palaeontological collection of the Queensland Museum (QMF)

and the palaeontological collection of the Bureau of Mineral Resources, Canberra (CPC). Cusp nomenclature follows Archer (1984) and Rich et al. (1978) except that what was then understood to be the hypocone of upper molars is now accepted to be the metacone following Tedford & Woodburne (1987). Molar homology follows Luckett (1993). Premolar homology follows Flower (1867). Higher level systematic nomenclature follows Aplin & Archer (1987).

SYSTEMATICS

Superorder MARSUPIALIA Illiger, 1811
Order DIPROTODONTIA Owen, 1866
Family DIPROTODONTIDAE Gill, 1872
Subfamily ZYGOMATURINAE Stirton,
Woodburne & Plane, 1967

Silvabestius gen. nov.

TYPE SPECIES. *Silvabestius johnnilandi* sp. nov.

OTHER SPECIES. *Silvabestius michaelbirti* sp. nov., Palorchestinae gen. and sp. indet. of Tedford (1967) (= *Silvabestius* sp. herein).

DIAGNOSIS. *Silvabestius* differs from other zygomaturines in the following combination of features: small parastyle on P³; absence of a deep trench separating parastyle from parametacone base on P³; absence of a well-developed lingual margin on upper molars; presence of upper canines (except *Neohelos*); absent or small

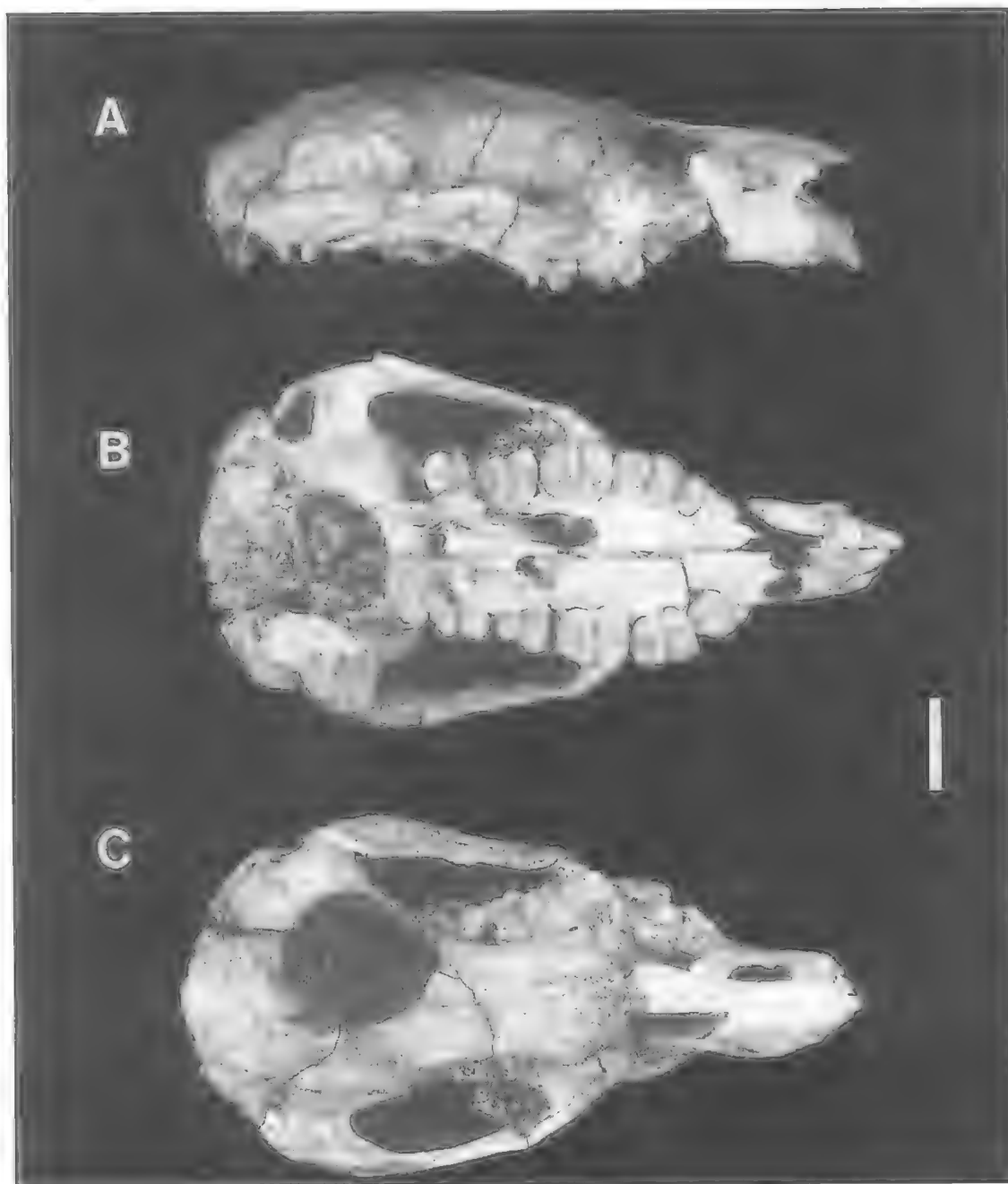


FIG. 1. *Silvestrius johnnili* gen. et sp. nov., holotype, QMF30504. A, right lateral view, B, ventral view, C, dorsal view. Bar = 20mm.

hypocone on P³ (except *Alkwertatherium webbi*); more anteriorly convex upper molar lochs (except for *Nimbadon*). It is distinguished from other zygomaturines except *Raemotherium yatkolai*

and *Nimbadon* by: its small size; molar gradient that does not appreciably increase posteriorly. It is distinguished from other zygomaturines except *Nimbadon* and *Neohelos* by: the anterobuccal

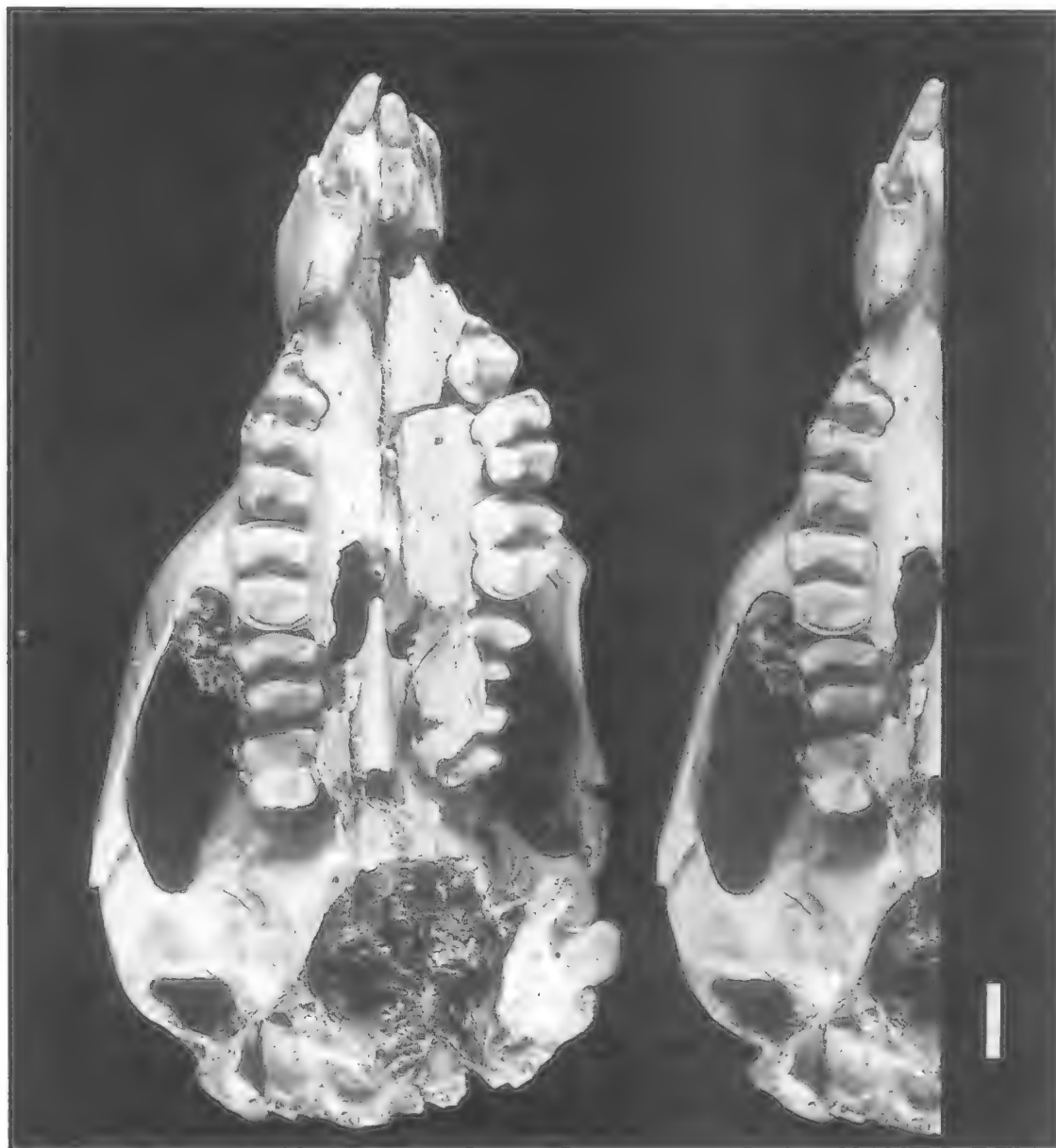


FIG. 2. *Silvabestius johnnilandi* gen. et sp. nov., holotype, QMF30504. Occlusal stereopair of upper cheektooth dentition. Bar = 10mm.

blade from the parametacone on P^3 ; absence of a well-developed buccal cingulum or metastyle on P^3 . It can be distinguished from other zygomaturines except *Neohelos*, *Nimbadon* and *A. webbi* by an undivided parametacone on P^3 .

ETYMOLOGY. Latin *silva*, forest and *bestia*, beast; for its inferred habitat; masculine.

***Silvabestius johnnilandi* sp. nov.**
(Figs 1-6)

MATERIAL. Holotype QMF30504, a juvenile skull and associated mandible with completely unworn left and right cheek tooth rows. The basicranium, palate and nasals are incomplete. Both dentaries are missing the coronoid process. I^{2-3} is missing on each side. P^3 and M^{3-4} on each side were unerupted at the time of



FIG. 3. *Silvestrius johnnilandi* gen. et sp. nov., right dentary of holotype QMF30504. Occlusal stereopair. Bar = 10mm.

death. Paratype QMF30505, a virtually complete adult skull; its frontals are broken and slightly depressed; a large fracture runs diagonally from the left orbit to the dorsal surface of the premaxilla and continues ventrally through the right canine alveolus and onto the palate. The right palatine bone is fractured and depressed. The left mastoid/paroccipital process is broken. The supraoccipital is incomplete. Both types from VIP Site which is 3m below D Site; the latter contains diprotodontoids some of which belong to genera that occur in the late Oligocene in the Etadunna Formation (Woodburne et al., 1994) and thus we assign VIP Site to the late Oligocene.

Although a juvenile the holotype has perfectly unworn dentition which maximises information about crown morphology and both the skull and lower jaws, whereas the paratype is only a skull.

ETYMOLOGY. For Professor John Niland, Vice Chancellor of the University of New South Wales who

has been a strong supporter of the Riversleigh Project and helped collect at Riversleigh.

RELATIONSHIP OF THE HOLOTYPE TO THE PARATYPE. We conclude that QMF30504 was a dependent pouch-young living on its mother's (QMF30505) milk because: 1) both specimens were in the same deposit, within 1m of each other; 2) the lack of wear on the teeth of QMF30504 most of which were still erupting and the lack of fusion of any of its cranial bones; 3) when the upper and lower cheek teeth of the juvenile are brought into occlusion, the upper and lower incisors do not meet, but are separated by a gap of approximately 6 mm, a gap appropriate to suit a mother's nipple. 4) LI^3 of the adult skull, which was thought to be missing, was found adjacent to the nose of the juvenile skull suggesting that the adult and juvenile died nose to nose, suggesting an emotional relationship.

DIAGNOSIS. This species differs from *S. michaelbirti* in the following combination of features: it is much larger; it has an expanded parastylar region on P^3 and more distinct parastyle; it has a more posterior parametacone on P^3 ; it has a larger protocone on P^3 that is also more distinctly separated from the base of the parametacone by a deep fissure; it has a small but distinct hypocone on P^3 ; and it has less steeply sloping surfaces on the protoloph and metaloph of M^{1-4} .

DESCRIPTION. Upper incisors. L and RI^1 in the Holotype; L, RI^{1-2} and LI^3 in the Paratype. I^1 large, curved, with a thick, rounded base tapering to its tip. Enamel confined to the anterolateral surfaces and the upper third of the distal surface. L and RI^1 convergent at their tips. I^2 small, sub-ovate, tapering anteriorly, with narrow anterior tip contacting the posterolateral face of I^1 , with crown dominated by a large, ovate wear facet. I^3 posterior and slightly lateral to I^2 , smaller than I^2 , with a triangular occlusal surface, with apex oriented anteromedially, with a wear facet on most of the occlusal surface.

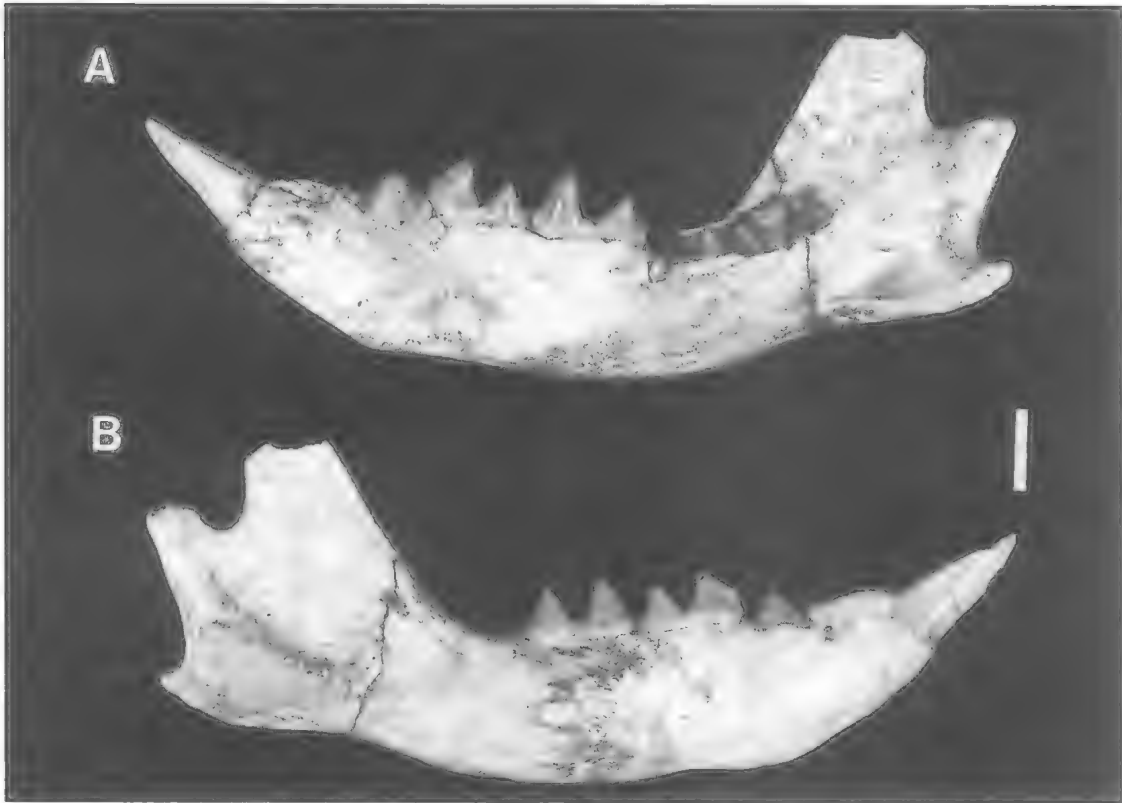


FIG. 4. *Silvabestius johnnilandi* gen. et sp. nov., right dentary of holotype QMF30504. A, lingual view. B, buccal view. Bar = 10mm.

Upper canines. Adult skull with small canine alveolus just posterior to the premaxillary/maxillary suture; obscured in the juvenile skull.

P³. Four cusps: a large parametacone; a well-developed protocone; a small distinct parastyle; and a poorly-developed hypocone. Widest across the protocone. Emargination between the bases of the protocone and lobate parastylar region defining the anterior and posterior moieties. Paratype premolar proportionately longer than that of the Holotype and the anterior and posterior moieties are more distinct. Large, undivided parametacone the tallest cusp on the premolar, situated along the midline of the tooth, slightly posterior to its transverse axis. Protocone large, lingually opposite the parametacone. Hypocone small but distinct, on the lingual cingulum at the posterolingual base of the protocone. Paratype P³ with extremely reduced and non-cusped hypocone.

Parametacone pyramidal in occlusal view with steep buccal, anterolingual and posterolingual faces. Each face defined by a distinct blade: an

anterior preparametacrasta, a posterior postparametacrasta and an anterolingually directed blade. Preparametacrasta linear, extending anteriorly (and slightly buccally) from the parametacone apex, continuous with a short, arcuate, posterobuccal blade from the parastyle. The anterolingually-oriented blade descending the anterolingual face of the parametacone, terminating in the fissure that separates the bases of the protocone and parametacone, just prior to meeting its counterpart, a short, linear, anterobuccally-directed protocone crest. A similar condition is found in *Nimbadon lavarackorum* (Hand et al., 1993a) and some *Neohelos* specimens from the Oligocene-Miocene of Riversleigh. In the paratype, the anterolingual parametacone blade is continuous with the anterolingual cingulum, a feature previously regarded as an autapomorphy of *Nimbadon* (Hand et al., 1993a). A slight swelling at the junction of the anterolingual blade and the lingual cingulum may represent a small protostyle.

TABLE 1. Measurements (mm) of *Silvabestius*. H=Height of crown; A/P=anterior-posterior length; Th=Thickness; W=width; IMP° = implantation angle; #=broken specimen; *=dimensions of alveoli.

A. I ¹ MEASUREMENTS					
Species	No	Side	H	A/P	W
johnnilandi	QMF 30504	L	7.1	-	6.5
		R	8.3	-	6.7
	QMF 30505	L	16.0#	8.7	6.9
		R	20.1#	8.3	6.9
michaelbirti	QMF 20493	L	18.9#	7.2	7.0
		R	18.3#	8.1	6.8
B. I ² MEASUREMENTS					
johnnilandi	QMF 30505	L	5.4	6.4	5.0
		R	5.4	6.3	5.1
michaelbirti	QMF 20493	L	-	5.9*	4.5*
		R	5.7	6.0	4.7
C. I ³ MEASUREMENTS					
johnnilandi	QMF 30505	L	4.7	5.3	4.1
		R	-	-	-
michaelbirti	QMF 20493	L	-	5.3*	4.8*
		R	-	5.2*	4.3*
D. UPPER CANINE MEASUREMENTS					
johnnilandi	QMF 30505	L	-	3.0*	2.2*
		R	-	3.2*	2.1*
michaelbirti	QMF 20493	L	6.3	5.1	3.5
		R	6.2	5.2	3.5
E. LOWER INCISOR MEASUREMENTS					
			Th	W	IMP°
johnnilandi	QMF 30504	L	7.0	4.7	30°
		R	8.1	4.6	30°

Postparametacrista well-developed, blade-like, continuous with the posterolingual cingulum.

Small, erect parastyle at the anterolingual corner, slightly buccal to the tooth margin, dominated by a distinct, arcuate blade continuous with the preparametacrista. Parastyle in paratype reduced to a slight swelling at the anterior tip of the preparametacrista. Short, ill-defined, anterolingual parastyle crest continuous with the anterolingual cingulum. Shallow anterolingual basin between the bases of the parastyle, parametacone and protocone, better defined in holotype RP³, but extremely shallow on the crown of the paratype.

Short, posteriorly-directed, apical protocone crest terminating 1/3 the way down its posterior surface. Two short, linear crests extending from the apex of the hypocone; one extending anteriorly and terminating at the posterior base of the protocone; other extending posteriorly, continu-

ous with the posterolingual cingulum. Buccal cingulum poorly-developed in the Holotype. Buccal surface of the parametacone with uniform, steep gradient to the base of the tooth crown. Well-developed buccal cingular shelf in the Paratype.

Upper molars. Proportionately similar to *Nimbadon whitelawi* from the mid-Miocene Bullock Creek Local Fauna (Hand et al., 1993a).

M¹. Sub-rectangular, low-crowned, transversely-bilophodont, with an anterior protoloph and posterior metaloph. Protoloph and metaloph short, anteriorly-convex crests, former slightly more arcuate than the latter; protoloph consisting of a buccal paracone and a lingual protocone; metaloph consisting of a buccal metacone and a lingual metaconule; metaconule the tallest cusp, followed by the paracone, metacone, then protocone. Parastyle small, at the anterobuccal end of the anterior cingulum, connected to an anterior paraconal crest by a short, posteriorly-oriented blade. Paratype parastyle poorly developed, slight swelling at the junction of the anterior paraconal crest and the anterior cingulum. Postmetacrista distinct, extending posteriorly from the metacone apex, continuous with the posterior cingulum. Metastyle a slight swelling at the posterobuccal margin, most reduced in the Paratype. Posterior cingulum terminating at the posterolingual base of the metaconule. Lingual cingulum in Holotype poorly developed, in Paratype short, crescentic, joining bases of the protocone and metaconule, blocking the lingual exit of the interloph valley. Short, indistinct, postparaconal crest descending the posterior face of the paracone, terminating in the interloph valley, before meeting its counterpart, an indistinct premetacrista. Short, linear, apical blade on the metaconule. Paratype with facets extending posterobuccally from the apices of the protocone and metaconule, fading down the posterior flanks of their respective cusps.

M²⁻⁴. Similar to M¹ except: Larger, proportionately wider anteriorly, with molars trapezoidal in occlusal view; paracone tallest cusp, protoloph higher than metaloph; parastyle and metastyle and their associated crests extremely reduced, as are the postparaconal crest and the premetacrista; lophs relatively longer, with protoloph longer than the metaloph, becoming more anteriorly convex in the more posterior molars; metaloph severely reduced, more obliquely oriented relative to the protoloph, with posterior moiety severely reduced. Molars increasing in size through M¹⁻², decreasing through M³⁻⁴. M⁴ reduced, lack-

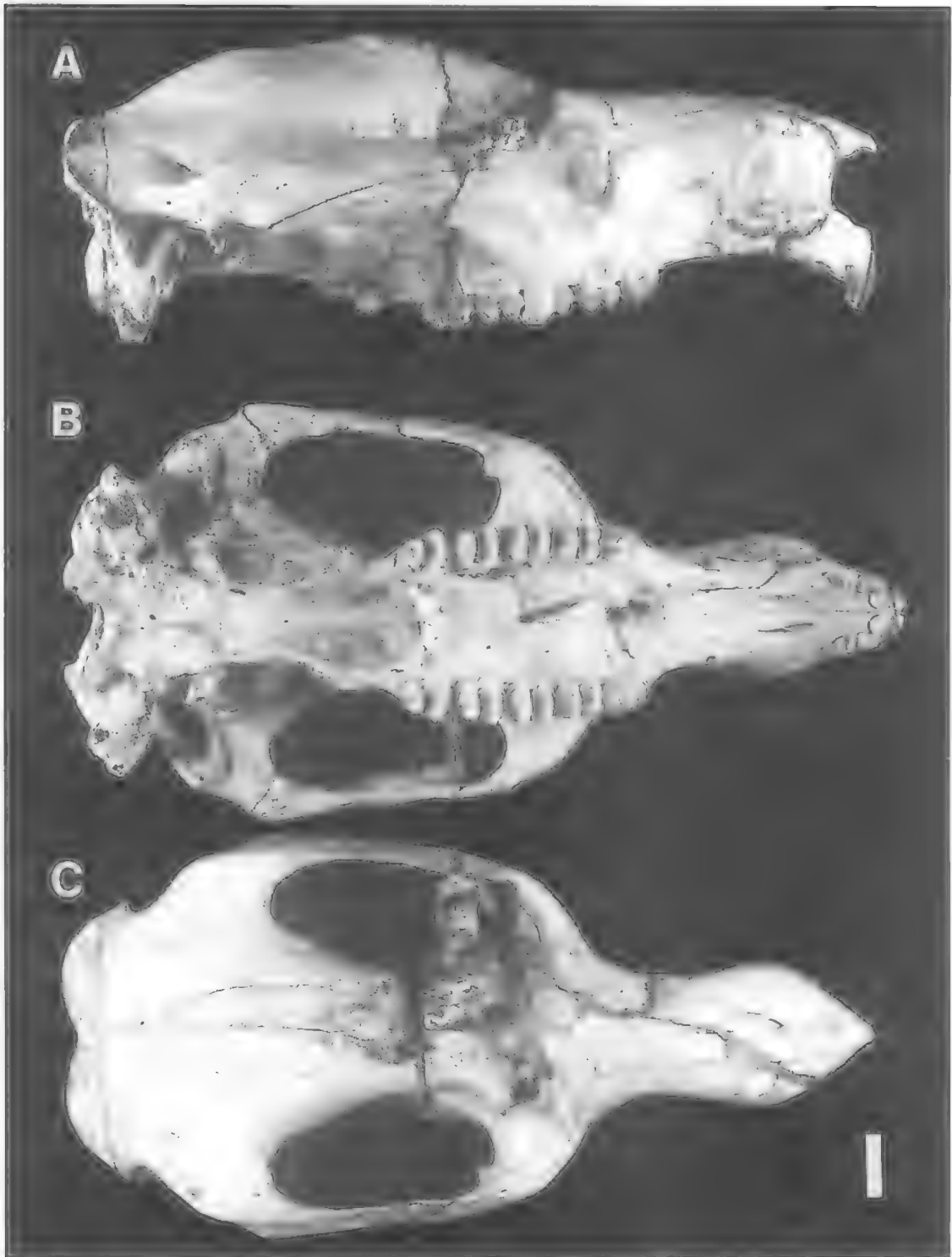


FIG.5. *Silwabestius johnniliandi* gen. et sp. nov., paratype QMF30505. A, right lateral view. B, ventral view. C, dorsal view. Bar = 20mm.

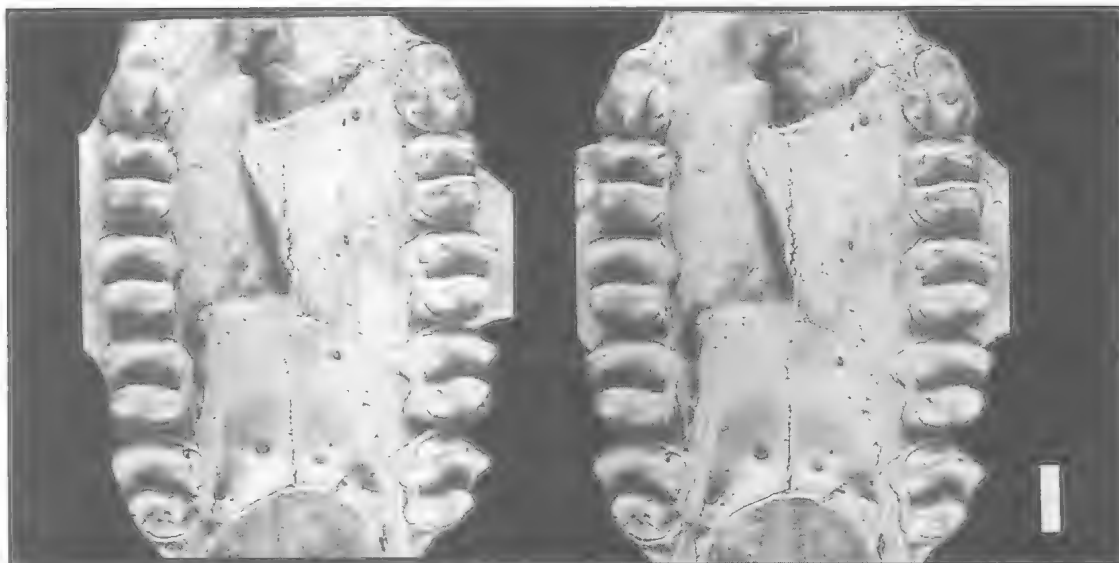


FIG. 6. *Silvestius johnniliandi* gen. et sp. nov., paratype, QMF30505. Occlusal stereopair of upper cheektooth dentition. Bar = 10mm.

ing enamel. Adult cheektooth row with an increasing molar gradient from M^1 to M^4 .

Lower dentition. A single pair of lanceolate, procumbent lower incisors in the Holotype. Enamel only on the lateral and ventral surfaces of the crown. A longitudinal groove occupying the internal dorsal surface, extending from the base of the incisor to the tip, approximately 2mm below and lingual to the dorsolateral tooth margin.

P_3 . Short, subovate, longer than wide, tapering anteriorly, dominated by a high, steep protoconid, with a short, steep, arcuate blade extending pos-

teriorly from the protoconid apex, terminating in a small cuspid on the posterior cingulid. A poorly defined crest descending the anterior face of the protoconid, terminating in a slight swelling at the anterior tooth margin. Posterobuccal cingulum poorly developed. Lingual cingulum curving around the posterolingual tooth margin, from the apex of the posteromedial cuspid to a point midway between the protoconid apex and posterior tooth margin. A vertical flanking crest descending the steep buccal face of the protoconid to a point just anterior to the terminus of the lingual cingulum.

TABLE 2. Measurements (mm) of *Silvestius*. L=length; AW=anterior width; PW=posterior width; *estimates.

A. UPPER CHEEK DENTITION																
Species	No.	Side	P3		M1			M2			M3			M4		
			L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
<i>johnniliandi</i>	QMF 30504	L	12.2	10.5	13.5	10.4	10.2	14.8	12.4	11.2	14.5	11.9	-	12.0	11.4	9.0
		R	11.7	10.7	13.6	10.6	10.2	14.5	12.5	11.4	14.3	12.9	10.8	11.5	11.8	9.1
	QMF 30505	L	13.1	11.0	14.4	11.9	11.5	14.7	13.2	11.8	15.2	13.2	11.4	15.3	12.8	9.8
		R	12.6	10.9	13.6	11.7	11.4	15.0	12.3	11.2	15.3	12.8	10.8	15.5	14.1	10.7
<i>michaelbirti</i>	QMF 20493	L	9.6	7.5*	10.4*	9.4*	9.0*	12.9	10.1*	9.2*	12.0	11.4*	9.8*	12.0	10.2	8.2
		R	9.6	8.3	11.3	9.7	9.3	11.0	10.4	9.6	11.9	10.3	8.7	11.3	10.2	8.1
sp.	CPC 7337	R	12.5	9.3	13.5	10.3	10.7	-	12.4	-						
B. LOWER CHEEK DENTITION																
<i>johnniliandi</i>	QMF 30504	L	10.8	7.1	13.5	8.1	8.9	14.6	9.6	10.0	14.6	11.3	9.6	12.7	-	9.2
		R	10.3	6.6	13.7	8.1	8.7	15.3	9.6	9.9	13.7	11.0	10.2	12.9	10.8	9.3

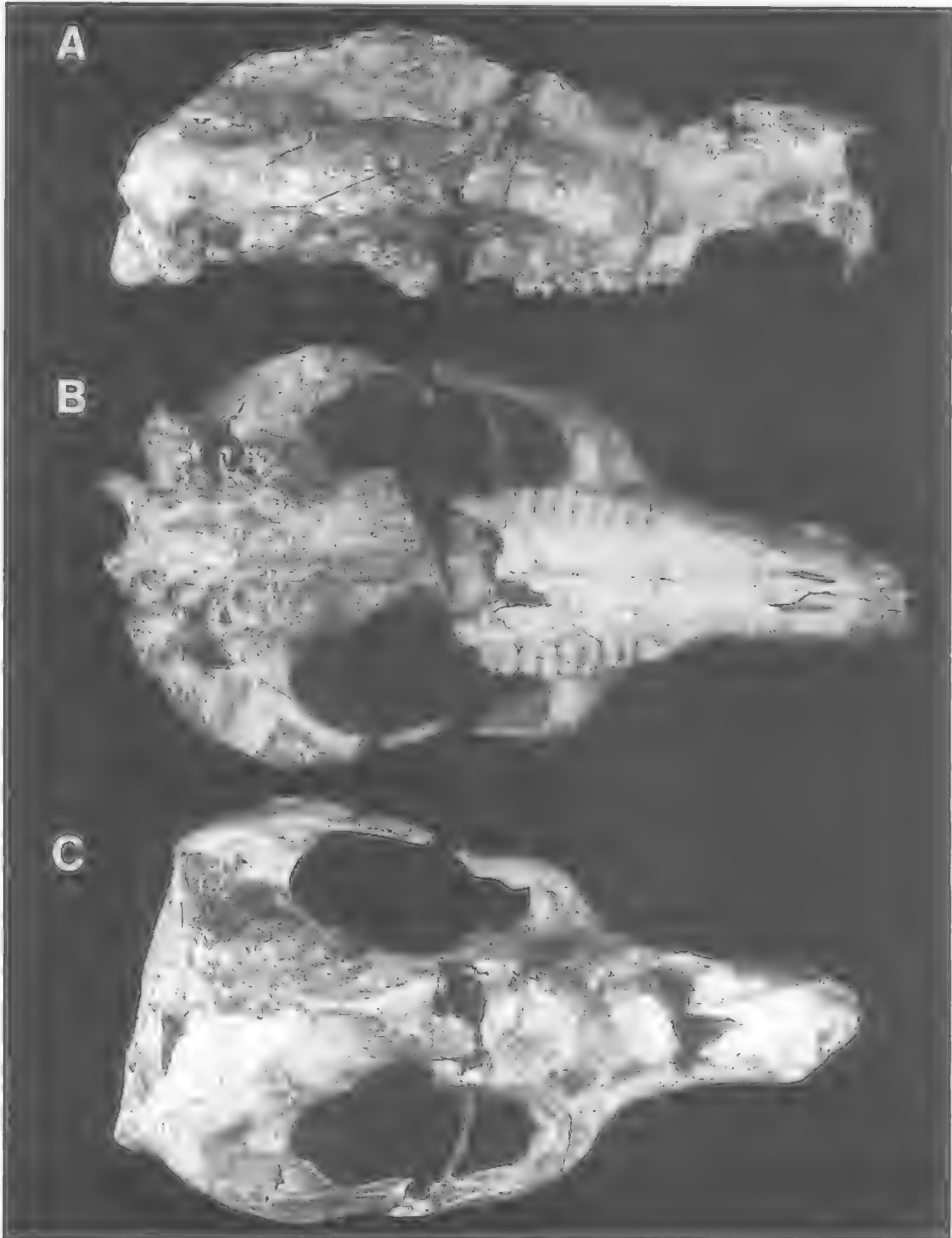


FIG. 7. *Silvestrius michaelbirti* sp. nov., holotype, QMF20493. A, right lateral view. B, ventral view. C, dorsal view. Bar = 20mm.

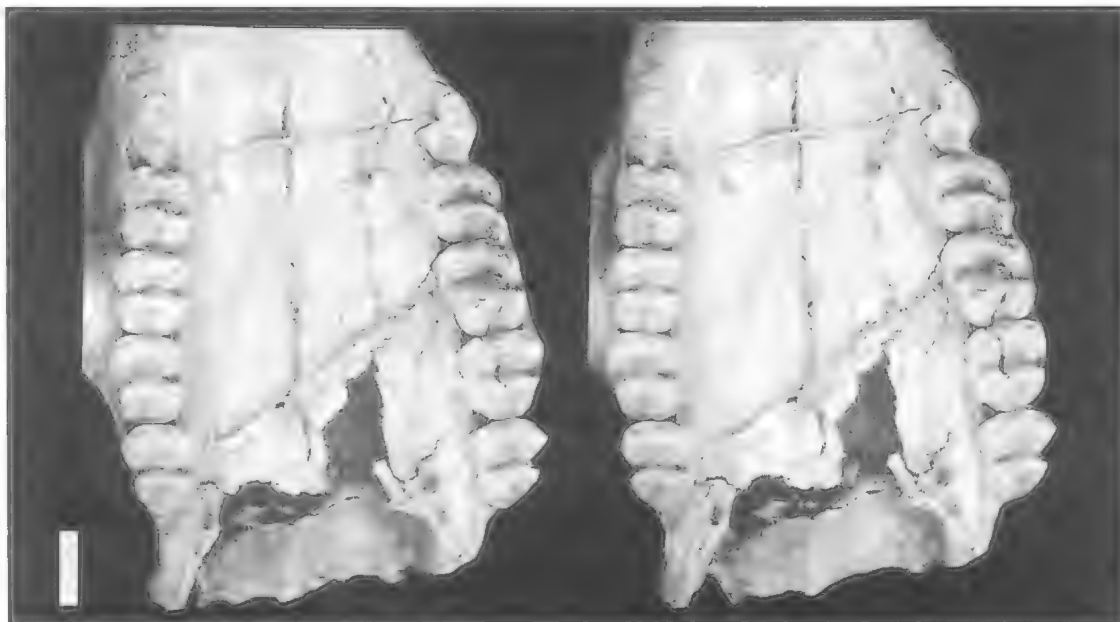


FIG. 8. *Silvestrius michaelbirti* sp. nov., holotype, QMF20493. Occlusal stereopair of upper cheektooth dentition. Bar = 10mm.

M₁. Subrectangular, anteriorly-tapering, transversely bilophodont. Anterior protolophid short, steep, high, running parallel to a steep, low, posterior hypolophid. Protoconid higher than metaconid; entoconid higher than the hypoconid. Paracristid anteriorly directed, blade-like, linking the protoconid to the anterior cingulum, slightly buccally convex. Anterior cingulum curving lingually and downward, to the base of the crown, meeting a relatively indistinct preprotocristid. Deep anterior basin defined by the junction of these crests and the anterior base of the protoconid. A short, vague crest fading down the posterobuccal base of the protoconid. Similar, better-defined crest fading down the posterior face of the metaconid. A well-developed, anterobuccally oriented prehypocristid terminating approximately 1/3 the way down the anterior face of the hypolophid. Lingual cingulum discontinuous, comprised of 2 ridges extending posterobuccally and posterolingually from the bases of the protoconid and hypoconid, respectively, with both ridges terminating just short of meeting each other in the interlophid valley. Similar short ridge at the posterobuccal base of the metaconid. Posterior cingulum short, not extending around the bases of the entoconid and hypoconid. Transverse valley U-shaped in lingual view.

M₂. Similar to M₁ in all aspects except: slightly larger; protolophid subequal to its hypolophid; protolophid and hypolophid transversely wider; paracristid and prehypocristid extremely reduced; all ridges associated with the main cusps reduced; anterior face of the protolophid steeper; anterior cingulum better-developed; anterior basin absent.

M₃₋₄. Only partially erupted, similar to M₂ in all aspects except: M₃ less elongate, but wider than M₂; M₄ reduced relative to M₂₋₃; hypolophid reduced relative to the protolophid, slightly offset relative to the protolophid, more posteriorly convex; interlophid valley more open and broadly U-shaped.

REMARKS. Variation in the hypocone is common among Oligo-Miocene zygomaticurines. In fact, hypocone-less variants have been recorded for species of *Neohelos* (Peter Murray pers. comm.) and *Nimbadon* (Hand et al., 1993a). The development of a hypocone has, in the past, served as a synapomorphy of the Zygomaticurinae. We have used this feature in the phylogenetic systematic analysis presented below because, although variable, it is generally a good indicator of phylogenetic relationships.

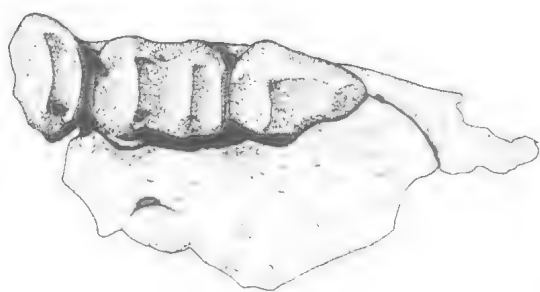


FIG. 9. *Silvestrius* sp., CPC7337, Occlusal view of right maxillary fragment with P³-M² from Site D Locality, Riversleigh. (After Tedford, 1967).

***Silvestrius michaelbirti* sp. nov.**
(Figs 7-8)

MATERIAL. Holotype QMF20493, a relatively complete cranium from late Oligocene Hiatus (South) Site (Creaser, 1997) with left and right cheek tooth rows; a longitudinal fracture runs through LM¹⁻³; RM¹ is fractured diagonally from the anterolingual tooth corner to the posterobuccal tooth corner; L and RI¹ are present

but incomplete; left I² and L and RI³ are missing; the cranium is in two parts, the division occurring approximately 15mm posterior to the molar rows; the nasals, frontals and palate are incomplete; the basicranium is relatively intact; the posterior region of the neurocranium is missing on each side.

ETYMOLOGY. For the former Vice Chancellor of the University of New South Wales, Professor Michael Birt, who assisted in the collection of specimens and helped meet the cost of preparation.

DIAGNOSIS. Differs from *S. johnniliandi* by: being smaller; having canines; having reduced parastyle and parastylar region on P³ and less elongate P³; having a more central parametacone on P³; having a smaller protocone on P³ that is less distinctly separated from the base of the parametacone; lacking a hypocone on P³; and having steeper protoloph and metaloph faces on M¹⁻⁴. Differs from *Silvestrius* sp. in: being higher crowned; lacking a well-developed parastylar region on P³; and having a reduced posterolingual cingular shelf on P³.

DESCRIPTION. This species is described in so far as it differs from other species of the genus. Incisor arcade poorly-preserved with only the L and R I¹ (both of which are incomplete) and the right I² remaining. Incisors as in *S. johnniliandi*.

Canines small, pointed, on the premaxillary-maxillary suture whereas in *S. johnniliandi* the tiny canine alveoli lie approximately 2mm behind the premaxillary-maxillary suture.

Left cheektooth row badly fractured with a large fissure extending across the buccal margin of M¹, diagonally through M² and across the lingual region of M³, terminating at the anterior base of the hypolophid of M³. Right M¹ fractured diagonally from the anterolingual tooth corner to the posterobuccal tooth corner.

P³ smaller, lacking a distinct cusped parastyle, with parastylar region reduced; vague preparametacrista continuous with the anterior cingulum; parametacone more posteriorly along the longitudinal axis, with postparametacrista more steeply inclined; protocone smaller, less distinctly separated from the base of the parametacone; hypocone absent; protocone without crests.

Upper molars. Lower-crowned, with more extensive wear facets, with more steeply inclined posterior surfaces of the protoloph and metaloph; with a molar gradient not increasing posteriorly.

TABLE 3. Character state polarities for selected zygomaturine genera using species of *Ngapakaldia* (Palorchestidae) as an outgroup. A=absent; P=present; S=small; D=distinct; W=weak; ST=strong; SQ=square; R=reduced; ==equal or subequal. PLESIO=plesiomorphic; APO=apomorphic.

CHARACTER	PLESIO-	APO-
1. Parastyle development on P ³	A	P
2. Hypocone development on P ³	A/S	D
3. Division of parametacone into two distinct cusps on P ³	A	P
4. Well-developed diagonal crest on parametacone of P ³	A	P
5. Link between protocone and parametacone on P ³	A/W	ST
6. Mesostyle retracted towards cingulum	A	P
7. Size of P ³ relative to equal molars	S	=
8. Elongate P ³	A	P
9. Buccal cingulum on P ³	ST	W
10. Loss, incorporation or suppression of stylar cusps C and D with respect to lophs	A	P
11. Small parastyle on M ¹	P	A
12. Occlusal shape of M ¹	E	SQ
13. Short posterior moiety on P ₃	P	A
14. Paracristid on M ₁	P	R

Ngapakaldia and *Pitikantia* as outgroup for analysis of the Zygomaturinae due to their plesiomorphic position in the Diprotodontoidea.

CHARACTER ANALYSIS. Fourteen dental characters considered taxonomically useful in zygomaturine intergeneric relationships are employed in a cladistic analysis (Table 4). Selection of characters follows previous phylogenetic analyses by Murray (1990b) and Hand et al. (1993a). Character state polarities (Table 3) were determined by outgroup analysis using *Ngapakaldia* and *Pitikantia*. Character state polarities for *Nimbadon* were scored only for *Ni. lavarackorum* and *Ni. whitelawi*, for reasons given in the discussion. *Raemeotherium yatkolai* was excluded from the phylogenetic analysis because 13 of the 14 characters are unknown for this species.

A Wagner analysis was performed using the PAUP (version 3.1.1) computer program (Swofford, 1993). Multistate characters were treated as polymorphisms. Character optimisation was performed using both the accelerated (ACCTRAN) and delayed (DELTRAN) transformation algorithms.

CHARACTERS EXCLUDED FROM THE ANALYSIS. For many characters examined from previous phylogenetic analyses, intraspecific and interspecific variation was found to be high. Similarly high variation is characteristic of the Oligo-Miocene zygomaturines *Neohelos* and *Alkwertatherium* (Murray, 1990b). Characters with a high degree of intraspecific variation excluded from the analysis include: the degree to which the parastyle of P³ is posteriorly inclined or 'hooked'; shape of the lingual cingulum on P³; presence or absence of a protostyle on M¹; extent of metaloph reduction on M³⁻⁴; extent of reduction of M⁴. 'Proportional similarity' of P³ as a synapomorphy for a *Plaisiodon*/*Nimbadon*/*Neohelos*/*Kolopsis*/*Zygomaturus* clade, used by Murray (1990b) and Hand et al. (1993a), is a character complex relating to the development of the parastyle, protocone and hypocone. Accordingly, it is not included as a discrete character.

RESULTS. Wagner analysis using the branch and bound algorithm generated a single most parsimonious tree (Fig. 11) involving 23 steps with a consistency index (CI) of 0.880, a retention index (RI) of 0.880 and a rescaled consistency index (RC) of 0.774. The high consistency index probably reflects the limited number of characters used in the analysis. Tree topology was iden-

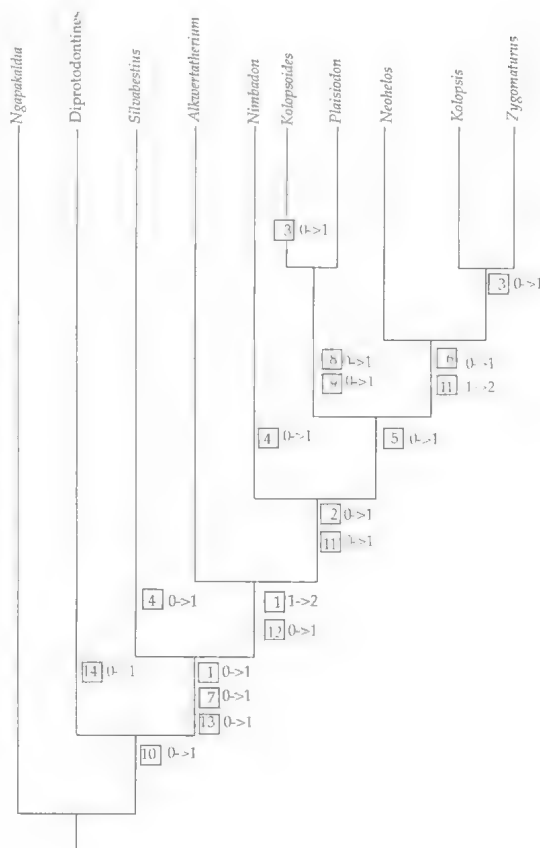


FIG. 11. Hypothesis of zygomaturine relationships, based on dental characters (Table 3) used by Murray (1990b) and Hand et al. (1993) in cladistic analyses of the Diprotodontidae. Apomorphies are represented by boxed numbers. Arrows indicate character state transformations. Symbols: 0, plesiomorphic character state; 1, derived character state; 2, most derived character state.

tical irrespective of whether ACCTRAN or DELTRAN character optimisation was employed.

DISCUSSION

Silvabestius is the most plesiomorphic zygomaturine known with the possible exception of *Raemeotherium yatkolai*. *Silvabestius* is basal to the diprotodontoid radiation. Although similar to the primitive palorchestid *Ngapakaldia* in dentition (Tedford, 1967) and the middle ear, *Silvabestius* is assigned to the Zygomaturinae because it possesses a number of zygomaturine

synapomorphies including a parastyle on P^3 and a ventral alisphenoid tympanic process.

Stirton et al. (1967) and Murray (1990b) suggested that zygomaturines evolved from primitive diprotodontine-like forms in which the parastyle on P^3 was small. Trends in premolar morphology in *Silvabestius* support this hypothesis. Transition from the simple, bicusped diprotodontine P^3 to the plesiomorphic, 3-cusped zygomaturine premolar of *S. michaelbirti* is achieved through expansion of the parastylar region (resulting in a more elongate premolar) and the posterolingual cingular shelf. Subsequent transition to the more typical 4-cusped zygomaturine premolar of *S. johnnilandi* is achieved through development of a distinct parastyle on the enlarged parastylar region and development of a distinct hypocone on the enlarged posterolingual cingular shelf.

Silvabestius is the plesiomorphic sister group to all other zygomaturines (Fig. 9). Plesiomorphic features of the dentition include a poorly-developed parastyle, a poorly-developed hypocone, an undivided parametacane on P^3 , and a well-developed paracristid on M_1 .

Monophyly of Zygomaturinae is supported by: a parastyle on P^3 ; P^3 equal or subequal to the molars in length; and an enlarged posterior moiety on P_3 . The zygomaturine sister-group of *Silvabestius* is united by synapomorphic a moderate to large parastyle on P^3 and square vs elongate molars (in occlusal view). A distinct hypocone on P^3 and a well-developed parastyle on M^1 are shared by *Nimbadon*, *Kolopsoides*, *Plaisiodon*, *Neohelos*, *Kolopsis* and *Zygomaturus*. The latter genera, with the exclusion of *Nimbadon*, is united by a linking crest between the apices of the protocone and parametacane on P^3 . *Kolopsoides* and *Plaisiodon* are united by an elongate P^3 and a weak buccal cingulum on P^3 . *Neohelos*, *Kolopsis* and *Zygomaturus* form a clade rationalised by a mesostyle that is retracted towards the cingulum on P^3 and by a large parastyle on M^1 . *Kolopsis* and *Zygomaturus* are united by a parametacane on P^3 that is divided into two distinct cusps.

Topology of the cladogram (Fig. 9) is consistent with that found in Hand et al. (1993a) and Murray (1990b). However, it differs in the relative positions of species of *Nimbadon*, *Plaisiodon* and *Kolopsoides*. These differences result from the exclusion of certain characters used in previous analyses which are of low taxonomic value. A hooked or posteriorly inclined parastyle on P^3 has been used by Murray (1990) and Hand et al.

(1993a) as a synapomorphy uniting *Plaisiodon* and *Nimbadon*. In this analysis the character was found to be highly variable and hence of low taxonomic value. No special affinity was found between *Nimbadon* and the *Kolopsoides/Plaisiodon* clade. Further, Hand et al. (1993a) united *Nimbadon*, *Plaisiodon*, *Neohelos*, *Kolopsis* and *Zygomaturus* to the exclusion of *Kolopsoides* by the similarly proportioned P^3 . This character was excluded from the current analysis because it was found to be dependent on the degree of development of the parastyle, protocone and metacone on P^3 .

The position of *Kolopsoides cultridens* within the Zygomaturinae is difficult to determine, partly because of the paucity of knowledge about late Miocene diprotodontoids. Stirton et al. (1967) suggested that *K. cultridens* is most closely related to *Kolopsis* on the basis of a divided parametacane on P^3 . Flannery (1994) suggested that all New Guinea diprotodontids, including *K. cultridens*, are closely related and probably stemmed from a *Kolopsis*-like ancestor. *K. cultridens* is here linked with the late Miocene *Plaisiodon centralis*, from the Alcoota Local Fauna, a relationship first proposed by Archer (1984). If this relationship is accepted a divided parametacane has developed within the Zygomaturinae in the *Kolopsoides/Plaisiodon* lineage and again, convergently, in the *Neohelos/Kolopsis/Zygomaturus* lineage. Homoplasious division of the parametacane into 2 distinct cusps would then have developed during the late Miocene perhaps in response to increasing dryness. With plant materials becoming less succulent and more abrasive, there may have been strong selective pressure on all lineages to increase molariform features as well as the surface area of premolars.

We suggest that *Nimbadon scottorum* is more appropriately assigned to *Neohelos*. Features of the dentition that align *Ni. scottorum* with *Neohelos* are: larger, squarer molars; more robust cingula on the cheekteeth; greater parastyle development on M^{1-2} ; a relatively erect parastyle on P^3 ; and an anterolingual crest extending from the parametacane apex that meets a buccal crest from the apex of the protocone (a feature common in species of *Neohelos*) rather than continuing on to meet the anterolingual cingulum as in *Ni. lavarackorum* and *Ni. whitelawi*. Material referable to a small species of *Neohelos* from Riversleigh's System A Local Faunas, and forms intermediate between this small *Neohelos* species and *N. tirarensis* from Riversleigh's System B Local Faunas, are relatively indistinguish-

able in terms of morphology and dimensions from the Holotype and only specimen of *Ni. scottorum*, QMF23157. Consequently, character polarities for species of *Nimbadon* in this analysis were determined using *Ni. lavarackorum* and *Ni. whitelawi* only.

Similarities in dentitions of *Silvabestius johnniliandi* and *Nimbadon lavarackorum*, both from Riversleigh, and *Ni. whitelawi*, from the Bullock Creek Local Fauna include: molar dimensions; structure of the parastylar region; protocone; hypocone; buccal cingulum; and anterolingual parametacone blade on P^3 . The last feature was suggested (Hand et al., 1993a) as an autapomorphy for *Nimbadon* but it is variably expressed in *Neohelos* and well-developed in *Silvabestius*. Dentitions of *S. johnniliandi* and *Nimbadon* differ mainly in the degree of development of the parastyle on P^3 and the extent to which it is separated from the base of the parametacone. Plesiomorphic features of *Nimbadon* include a small parastyle and undivided parametacone on P^3 , elongate vs relatively squarish molars, and a well-developed paracristid on M_1 .

Murray (1990b) suggested that *Nimbadon* may be a basal zygomatuline with affinity to *Neohelos* and *Platysiodon*; he suggested 2 minor zygomatuline lineages, *Nimbadon*, *Neohelos* and *Kolopsis*, united largely through plesiomorphic features and *Alkwertatherium*, *Platysiodon* and *Kolopsoides*, united through phenetic similarities of the dentary and lower incisors. He also suggests that these lineages may be united through common ancestry in *Nimbadon*. In our analysis *Nimbadon* occupies a more plesiomorphic position than in other analyses.

Some doubt remains about whether *Raemerotherium yatkolai* is appropriately included within Diprotodontidae. Rich et al. (1978) noted that it exhibited no apomorphic character states that precluded the possibility that it was a primitive macropodoid but, equally, neither does it exhibit any character states that are undoubted macropodoid synapomorphies. The relative phylogenetic positions of *Silvabestius* and *Raemerotherium* cannot be resolved until upper dentitions are discovered for the latter. Differences in the lower dentition of *S. johnniliandi* compared with *R. yatkolai* include: it is larger; lophids on the lower molars are less anteriorly convex; the anterior moiety of M_1 is broader; the premetacristid of M_1 is better developed as is the anterolingual basin at the anterior base of the protolephid; the protostylid (Rich et al., 1978) at the buccal base of the protoconid on M_1 is absent; and the pru-

tolophid on M_1 is more posteriorly inclined. Both species exhibit an $M_1:M_3$ ratio (equivalent to $M_2:M_4$ in Rich et al., 1978) approaching 1, a condition regarded as primitive among diprotodontoids. There are no apomorphic features of the lower dentitions that enable either to be regarded as unambiguously more plesiomorphic than the other.

Silvabestius johnniliandi is derived relative to *S. michaelbirti* as evidenced by the following features of its P^3 : a more distinct parastyle; a larger, lobate parastylar region; a better defined preparametacrista; and a small but distinct hypocone. The relative position of *Silvabestius* sp. is more difficult to determine because of poor preservation. However, the following features of the dentine core suggest that *Silvabestius* sp. is structurally intermediate between *S. michaelbirti* and *S. johnniliandi*: parastylar region more extensive than *S. michaelbirti* but reduced in comparison to *S. johnniliandi*; hypocone absent in *S. michaelbirti*, a more extensive posterolingual cingular shelf in *S. sp.*, a feature that anticipates the development of a hypocone in *S. johnniliandi*. *Silvabestius* sp. has no autapomorphic features in the dentition that would preclude it being the ancestor of *S. johnniliandi*. Alternatively, *Silvabestius* sp. may represent an extreme end of an *S. johnniliandi* morphocline. If this is the case, the simple dental structure of *S. michaelbirti* and the absence of any autapomorphic features of the dentition, suggest this species may represent the direct ancestor of *S. johnniliandi* and the structural antecedent of all other zygomatulines.

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NIMIOKOALA GEN. NOV. (MARSUPIALIA, PHASCOLARCTIDAE) FROM
RIVERSLEIGH, NORTHWESTERN QUEENSLAND, WITH A REVISION OF
LITOKOALA

K. BLACK AND M. ARCHER

Black, K. & Archer, M., 1997:06:30. *Nimiokoala* gen. nov. (Marsupialia, Phascolarctidae) from Riversleigh, northwestern Queensland, with a revision of *Litokoala*. *Memoirs of the Queensland Museum* 41(2): 209-228. Brisbane, ISSN 0079-8835.

The early to middle Miocene phascolarctid *Nimiokoala greystanesi* gen. et sp. nov. is described from Riversleigh, northwestern Queensland. *Nimiokoala* sp. is recognised from a late Oligocene deposit in South Australia. The complex molar morphology and plesiomorphic basicranial morphology of *Nimiokoala* are indicative of a more diverse infraorder of phascolarctomorphians. Similarities in molar morphology between *Nimiokoala* and ektopodontids are noted and may reflect similar ecological niche. *Litokoala kamunkaensis* is described from the Miocene of Riversleigh extending its range and distribution. Cladistic analyses of dental characters of all living and extinct taxa support the intrafamilial relationships proposed by Woodburne et al. (1987a). *Litokoala* is identified as the sister group of the modern genus and *Nimiokoala* is most closely related to the *Litokoala*/*Phascolarctos* clade. □ *Phascolarctidae*, *Nimiokoala*, *Litokoala*, *Oligocene*, *Miocene*, *Riversleigh*.

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A partial skull, representing a small, highly specialised phascolarctid was collected from Boid Site East, System B deposits (Archer et al., 1989; 1991), Riversleigh, northwestern Queensland. Based on a superficial analysis of dental morphology, the skull was incorrectly figured by Archer et al. (1991) as a new species of the Miocene phascolarctid *Litokoala*. Two species of *Litokoala* were known: *L. kutjamarpens* (Stirton et al., 1967) from the Kutjamarpu Local Fauna, Wipajiri Formation, Lake Ngapakaldi, South Australia (known from a single upper molar) and *L. kamunkaensis* (Springer, 1987) from the Kanunka North Local Fauna, Eladunna Formation, South Australia (known from 2 isolated teeth and some molar fragments).

N. greystanesi gen. et sp. nov. is similar to *Litokoala* but its generic separation is substantiated by comparison with new material (an M³ and a lower dentition) of *L. kamunkaensis* from System C (Archer et al., 1989; 1991) at Riversleigh. A further new species of *Nimiokoala* is recognised from South Prospect B Locality, Lake Namba, Frome Downs Station, South Australia.

The moderate abundance of *N. greystanesi* in Riversleigh deposits contrasts with the paucity of material of other phascolarctids which are known from isolated teeth or, at best, dentitions. This paper describes dentition of the new genus and analyses phascolarctid phylogeny based on dental characters.

Suprageneric nomenclature follows Aplin &

Archer (1987). Dental terminology follows Archer (1978b) except that what was then understood to be the hypocone of upper molars is now accepted to be the metacone (Tedford & Woodburne, 1987). Cheek tooth homology is that proposed by Luckett (1993). Biostratigraphic nomenclature follows Woodburne et al. (1993). Archer et al. (1989) and Archer et al. (1991). Specimens referred to are housed in the following repositories: Queensland Museum (QMF), South Australian Museum (SAMP), University of California at Riverside (UCR). Measurements were made using a Wild M5 microscope with digital length measuring set.

SYSTEMATICS

Order DIPROTODONTIA Owen, 1866
Suborder VOMBATIFORMES Woodburne, 1984

Infraorder PHASCOLARCTOMORPHIA
Aplin & Archer, 1987

Family PHASCOLARCTIDAE Owen, 1839

Nimiokoala gen. nov.

TYPE SPECIES. *Nimiokoala greystanesi* sp. nov.

ADDITIONAL SPECIES. *Nimiokoala* sp.

DIAGNOSIS. *Nimiokoala* differ from all other phascolarctids in: being smaller (except species

of *Litokoala*): having a large, cuspsate parastyle which is pyramidal in occlusal view (except *Litokoala kutjampensis*); a well-developed, crescentic paraconule and neometaconule on M_1 - M_4 , the latter of which is double cusped in the more posterior molars; a more reduced metacone and metaconule on M_1 and a more rounded posterior margin of that tooth.

Robust, ridge-like crenulations; strong posterobuccal ridges from the apices of the protocone and metaconule; a discontinuous neometaconule subdivided into two or more parts and a (variably) discontinuous paraconule; a posterolingual cusp on P_3 ; a well-developed posterolingual crest from the apex of the protostylid on M_1 ; a weaker metastylid; a well-developed neomorphic cuspid occupying the trigonid basin between the metaconid and protoconid on M_2 - M_4 ; an anterobuccally directed pre-entocristid (as opposed to anterolingually directed in other phascolarctids); a well-developed cuspsate entostylid ridge; and a more posterobuccally directed postprotostylid cristid.

Nimiokoala greystanesi differs from *Koobor* in: being higher crowned; lacking the bicusped P_3 ; having strong posterolingual paracristae and posterolingual metacristae; having a protostyle; and in having reduced styler cusps and from *Madakoala* in: being higher crowned; more crenulated; in having a more cuspsate, isolated posterolingual cusp on P_3 and in lacking the lingual cingular ridge of that tooth (in *M. sp. cf. M. wellsii*); having wider, less elongate upper molars; a more buccal junction of the premetacristae and postparacristae; a well-developed protostyle; relatively smaller buccal surfaces of the paracone and metacone; lacking the transverse connection between the metacone and metaconule on M_4 ; having a less elongate P_3 that consists of three main apices (as opposed to four in *Madakoala*), a small posterolingual cuspsule and a proportionately larger, more isolated posterobuccal cusp on that tooth; lacking the well-developed buccal and lingual crests from the main apices of P_3 ; having a larger, more cuspsate protostylid on M_1 ; a more lingually situated protoconid and a more lingual junction of the cristid obliqua and postprotocristid in the M_1 ; a well-developed anterobuccal ridge off the entoconid apex; and in lacking the hypoconid-entoconid crest on M_2 - M_4 .

Nimiokoala differs from *Perikoala* in being less crenulated; lacking the lingual shelf basal to the metaconid and entoconid on the lower molars; and in those features listed for *Madakoala*.

Nimiokoala differs from *Litokoala*,

Phascolarctos and *Cundokoala yorkensis* in: having a bulbous, less trenchant P_3 ; lacking the bulbous cuspsule at the anterolingual base of the metaconule of M_1 (M_1 unknown for *L. kamunkaensis*) and the resultant pocket developed between the premetaconule crista, postprotocrista and the lingual margin; lacking the anterolingual protocone crest on M_1 ; lacking a metastylid fold; lacking buccal ribs on the protoconid, metaconid and entoconid; having a discontinuous lingual ectolophid wherein the postmetacristid and preentocristid do not meet; having a weaker entostylid; and in having less separation between the protoconid and paraconid on M_1 (M_1 unknown for *L. kutjampensis*).

Nimiokoala greystanesi differs from *L. kutjampensis* in lacking the buccal extension connecting the paraconule to the buccal margin. *Nimiokoala* differs from *L. kamunkaensis* in: having a posterolingual cuspid on P_3 ; a greater separation of the anterior and posterior apices of P_3 and a more cuspsate anterior apex of that tooth; lacking the lingual and buccal ribs from the main apices on P_3 ; lacking an entoconid lingual shelf (postentostylid cristid) and metaconid lingual shelf; and in lacking a posterolingual protoconid ridge on M_4 .

Nimiokoala differs from *Phascolarctos* and *Cundokoala yorkensis* in: having a large posterolingual cusp on P_3 and strong anterior, buccal and lingual crests that extend from the anterior apex of that tooth; lacking the lingual cingular ridge of P_3 ; having proportionately wider upper molars; lacking the pocket at the anterior base of the protocone on M_1 ; having a proportionately less elongate P_3 ; having a large posterobuccal cusp on P_3 and strong anterior and buccal crests extending from the most anterior apex of that tooth; having a preprotostylid cristid on M_1 that is not continuous with the anterior cingulum; lacking the transverse connection between the apices of the metaconid and protoconid on M_2 ; lacking the columnar stylids of the metaconid and entoconid on M_1 - M_4 ; and in lacking the lingual ridge connecting the bases of the protoconid and hypoconid on M_2 - M_4 .

REMARKS. *Nimiokoala* sp. is known only from a dentary fragment with M_2 - M_4 . Comparisons involving the upper teeth of this genus are therefore confined to features of *N. greystanesi* sp. nov.

ETYMOLOGY. Latin *nimio*, excessive; refers to the complex molar morphology relative to other phascolarctids.

Nimiokoala greystanesi sp. nov.
(Figs 1-3; Table 1)

ETYMOLOGY. For Greystanes High School, winner of the Sydney Morning Herald/ Riversleigh competition.

MATERIAL. Holotype QMF30482, cranial fragment with parts of the left and right maxillae, jugals and palatine, part of left premaxilla and part of right frontal. The left alveoli of I^{1-3} , P^3 , M^{1-3} and right P^3 , M^{1-2} , from Neville's Garden Site, System B (Archer et al., 1989); early to middle Miocene. Other material: Boid site east - QMF30483 partial skull with the left and right premaxillae, nasals, palatine, part of the left and right jugals, right frontal, part of right parietal, part of basisphenoid and basioccipital, part of right tympanic bulla, left I^{1-3} , C^1 , P^3 and anterior half of M^1 , right I^1 , alveoli of I^{2-3} , alveolus of C^1 , P^3 (missing buccal margin) and M^1 (which is missing the enamel from the parastylar corner); QMF30484, right M^{2-4} ; QMF30485, left M^2 ; QMF30486, left M^2 fragment with posterior part of metaconule and the neometaconule preserved; QMF30487, right dentary fragment with alveolus of I_1 , broken P_3 , M^{1-4} ; Neville's Garden Site - QMF30512, right M^1 ; QMF23026, left M^2 ; QMF24232, left M^2 ; QMF24267, right M^2 ; QMF24233, left M^4 ; QMF20901, left M^4 and right M^4 ; QMF23027, left M^4 and right M^4 ; QMF29624, right dentary with P_3 , M^{1-3} ; QMF30488, left M_1 ; QMF30489, right M_1 ; QMF24266, right M_1 ; QMF24265, right M_2 ; QMF20903, left M_2 ; Camel Sputum Site - QMF30490, left P^3 ; QMF30491, left dentary with I_1 , alveolus of P_3 and alveolus of M^{1-2} ; QMF30492, broken right M_3 ; QMF24351, right P_3 ; Inabeyance Site - QMF30493, left dentary fragment with I_1 , P_3 , M^{1-2} , M_3 missing the anterobuccal corner, M_4 missing the buccal margin of the protoconid and the posterobuccal tooth corner. Dirk's Towers Site - QMF24516, molar fragment; QMF24291, left M^2 fragment; Rat Vomit Site - QMF30494, left dentary fragment with P_3 , M^{1-3} (all missing the lingual margin), and alveolus of M_4 . Upper Site - QMF30495, left P^3 ; QMF30496, right P^3 ; QMF30497, right M^3 . RSO Site - QMF30498, left M^3 ; QMF30499, talonid of M_3 .

DIAGNOSIS. *N. greystanesi* differs from *Nimiokoala* sp. in having: less rounded lower molars; less lingually sloping surfaces of the metaconid and entoconid; a slightly larger entostylid ridge; a larger neomorphic cuspid in the trigonid basin in M^{2-4} ; and a lesser reduction of the talonid in M_4 .

DESCRIPTION. Incisors. Left and right I^1 of QMF30483 short, pointed, with convergent tips, with enamel restricted to the anterior tooth face, with posterolingual faces dominated by large, triangular wear facets. Left I^2 small, subovate in

occlusal view, tapering anterolingually, without enamel on the occlusal surface. Left I^3 small, pointed, peg-like, contacting posterobuccal corner of the left I^2 , with enamel preserved on the buccal face.

Canines. Left canine short, peg-like, approximately 4mm behind the upper incisor arcade.

P^3 . LP^3 relatively robust, bulbous, wider posteriorly than anteriorly, with 5 major cusps, 3 of which lie along a slightly crescentic longitudinal crest with an additional posterobuccal and posterolingual cusp. The anterior most cusp 1.61mm posterior to the anterior tooth margin. Prominent crests extending anteriorly, posteriorly and buccally from its apex; anterior crest bifurcating into anterior and posterolingual spurs; spurs extending towards the base of the crown. Medial cusp separated from the anterior cusp by a deep crevice, connected to the posterior cusp by a short longitudinal crest. Apex of the medial cusp 2.32mm posterior to the anterior tooth margin. Well-developed crest extending anterobuccally from the medial apex, fading into the base of the crown. Posterior cusp 3.19mm behind anterior tooth margin, with well-developed posterior crest extending from its apex; bifurcating at the base of the cusp, with one arm continuing posteriorly and fading into the base of the crown; other cingulum-like arm curving around the lingual tooth margin, connecting to the posterior crest of the well-developed posterolingual cusp. Posterolingual cusp apex opposite and slightly posterior to the medial cusp, with an anterolingual ridge fading into the lingual base of the crown from the apex. Posterobuccal cusp opposite, but slightly anterior to the posterior apex, with a well-developed crest extending posterobuccally from the apex, and fading into the base of the crown. An additional small cusplule at the anterior base of the posterolingual cusp.

RP^3 similar to LP^3 , but with less worn, medial cusp, smaller posterolingual cusp having weaker posterior crest extending from below the cusp apex and more distinct posterobuccal cusp.

Upper premolars (QMF30490, QMF30495, QMF30496) resemble P^3 of the holotype except for: buccal and lingual crests of the anterior cusp, the anterobuccal crest of the medial cusp and the posterobuccal crest of the posterobuccal cusp are reduced in QMF30495; undivided posterior crest of the posterior cusp fading into the anterior base of the crown in QMF30495, QMF30490 and QMF30496; small cusplule at the anterior base of the posterolingual cusp absent in QMF30495 and

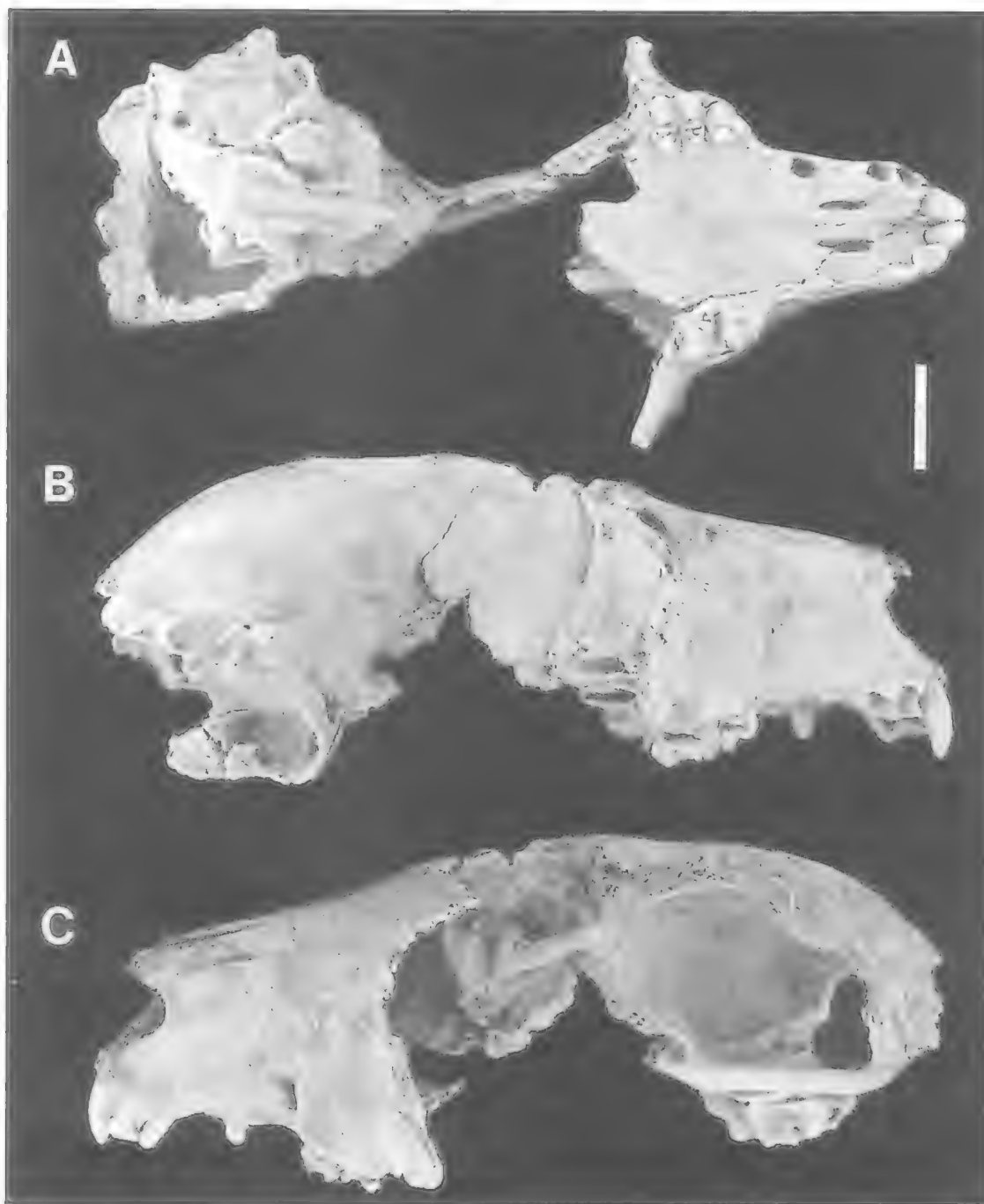


FIG. 1. Partial skull of *Nimiokoala greystanesi* gen. et sp. nov., QMF30483: A, ventral view; B, right lateral view; C, left lateral view. Bar = 10mm.

QMF30496; enamel missing from most of the occlusal surface of larger QMF30490 with re-

duced buccal crest of the anterior cusp, terminating before reaching the base of the crown.

M¹. Buccal margin of left M¹ slightly concave,

sloping anterolingually opposite the metacone; apices of the metacone and paracone slightly overhanging their lingual bases; lingual bases of paracone and metacone more lingually sloping in QMF30483 and QMF30512 than in the holotype; metacone taller than paracone; metaconule taller than protocone; parastylar corner, posterior and anterior base of metacone, posterior base of paracone, buccal bases of protocone and metaconule, lingual bases of paraconule and neometaconule and transverse valley crenulated. Paraconule well-developed, crescentic, cuspsate, occupying the longitudinal valley between paracone and protocone, bifurcate anteriorly; main arm extending anterobuccally and connecting to the anterolingual base of the parastylar corner, with two shorter, anteriorly directed spurs terminating at the base of the anterior cingulum and meeting the anterior cingulum in QMF30483. Posteriorly paraconule connecting to a strong posterolingual paraerista and a well-developed crest extending posterobuccally from the protocone apex; this connection more advanced in LM²⁻³. Paraconule not bifurcate posteriorly in RM¹ of holotype (or in QMF30483) but connecting to the posterolingual paraerista. Posteriorly bifurcate paraconule in QMF30512 without connection to the posterobuccal protocone crest. Large, crescentic, bicuspsate neometaconule occupying longitudinal valley between metacone and metaconule in M¹. Neometaconule in LM²⁻³ divided into two distinct cuspsate V-shaped structures. Neometaconule highly variable. In LM¹ of holotype connected to premetaconule crista by short anterior spur (not in RM¹), with second spur extending anterobuccally from the neometaconule and terminating in the transverse valley. In QMF30512 anterobuccal arm continuous with well-developed transverse ridges occupying the transverse valley of that tooth. Neometaconule connecting to anterolingual metaerista in RM¹ of QMF30483. Bifurcating posteriorly in LM¹ of the holotype: short posterolingually directed spur meeting a well-developed crest extending posterobuccally from the metaconule apex (these structures not meeting in RM¹ of the holotype); main arm of the neometaconule extending posterobuccally, meeting both the posterolingual metaerista and the posterior cingulum. Neometaconule not meeting posterolingual metaerista or posterior cingulum in QMF30483 and QMF30512. Slightly crescentic preparaerista extending anterobuccally from the paracone apex to the buccal margin, bifurcating, with one arm continuing anterobuccally to

meet the postparastylar erista; second arm extending posterobuccally, connecting with stylar cusp B. Slightly longer postparaerista bifurcating at the buccal margin; with one arm continuing posterobuccally to meet the premetaerista at the buccal margin; with second arm extending anterobuccally to meet stylar cusp C at buccal tooth margin. Paracone buccal basin closed on M¹ of holotype, variably closed in other specimens. Metacone with stylar cusps D and E reduced (stronger on QMF30512); with buccal basin shallow and open. Height of the stylar cusps decreasing progressively from the parastyle to E. Strong posterolingual paraeristae, anterolingual metaeristae and posterolingual metaerista in the upper molars of the holotype. Anterolingual paraeristae in QMF30512, QMF20901 and QMF23027. Protocone apex opposite but slightly posterior to the paracone apex, slightly lingual relative to the metaconule apex. Crescentic postprotocrista and premetaconule crista meeting in the transverse valley well buccal to the lingual tooth margin. A series of short spurs extending buccally from this junction, terminate in the transverse median valley. Protostyle well-developed, at the anterobuccal base of the protocone, extending posteriorly from the preprotocrista, terminating at the buccal base of the protocone opposite the apex of the paraconule. Surface enamel crenulations in the transverse valley of the LM¹ aligned into two parallel (discontinuous) transverse crests, contrasting with the reticulate pattern in RM¹ and more posterior molars of holotype. Distinct transverse crests occupying the transverse valley in QMF30483 and QMF30498.

M²⁻³. Similar in most aspects to LM¹ except for: teeth tapering more posteriorly, triangular buccal surfaces of the paracone and metacone sloping more steeply to the buccal margin; buccal margin more concave, buccal margin of the metacone sloping more posterolingually; parastyle absent; more reticulate crenulations; reduced stylar cusps; a deep pocket formed by the junction of the premetaconule crista, postprotocrista, the posterobuccal crest of the protocone and the posterolingual arm of the paraconule; protostyle reduced, connecting to the paraconule; neometaconule reduced, divided into 2 distinct V-shaped structures; neometaconule meeting anterolingual metaerista; a vague anterolingual paraerista in LM²⁻³.

M⁴ (Fig. 2B). Paracone, paraconule and protocone at similar stage of development to M¹ of the holotype. Metacone and metaconule ex-

tremely reduced to small cuspules on the posterobuccal and posterolingual margins, respectively. Posterior margin crescentic, consisting of a series of ridges extending anteriorly into the transverse valley. Premetacrista forming part of the posterior margin, curving anterobuccally around the tooth margin to meet the postparacrista at the buccal exit of the transverse valley. Neometaconule reduced, indistinguishable from the enamel crenulations.

Right dentition of the holotype similar to the left except for: smaller RM^1 ; less convex buccal margin; paracone and metacone sloping more gently to the buccal margin; deeper and less crenulated transverse valley lacking parallel transverse ridges; protocone higher than the metaconule; paraconule and neometaconule taller and less crescentic; paraconule apex closer to the protocone, not bifurcate anteriorly, without connection to the posterobuccal crest of the protocone; neometaconule not bifurcate anteriorly; protostyle weaker; anterolingual paracrista vaguely developed in the right M^1 .

LOWER DENTITION (Figs 2C, 3A-C). I_1 . Incisor narrow, lanceolate, with enamel covering ventral and buccal surfaces of the anterior half, with fine shallow longitudinal groove linearly along the buccal margin terminating approximately 1 mm posterior to anterior tip of tooth.

P_3 . LP_3 small, short longitudinally, of 3 aligned main cusps (anterior, medial and posterior), a large posterobuccal cusp and a small posterolingual cusp; lingual surface sloping steeply to the lingual tooth margin; shallow crevice separating the anterior cusp from the medial cusp; medial apex connected to the posterior cusp by a short longitudinal crest; prominent anterolingually directed crest and posterobuccally directed crest extending from the anterior apex and fading into the base of the crown; prominent crest connecting posterior cusp to posterior cingulum; apex of the posterobuccal cusp opposite and slightly posterior to the posterior cusp. Short anterobuccally and posterolingually directed crests extending from the apex of the posterobuccal cusp.

Lower molars distorted, with metaconid and entoconid anteriorly displaced relative to the protoconid and hypoconid, respectively.

M_1 . Subrectangular, anteriorly attenuated; hypoconid largest cusp on the talonid; protoconid largest cusp on the trigonid; well-developed protostylid at the buccal margin, opposite and slightly posterior to the protoconid apex. Pro-

tostylid and hypoconid pyramidal in occlusal outline in QMF30493 but more rounded in QMF30494. Preprotocristid extending anterolingually from the protoconid apex to a relatively small paraconid at the anterolingual corner (in QMF30488 paraconid connected to the premetacristid by a short longitudinal crest). Premetacristid poorly developed. Linear postprotocristid extending posteriorly into the central basin, meeting the crenulated cristid obliqua slightly lingual to the longitudinal tooth axis; postmetacristid extending posterolingually towards the weakly developed metastylid at the lingual tooth margin, with a well-developed posterolingually directed ridge branching off and extending into the transverse valley separating the talonid and trigonid. Crescentic preprotostylid cristid curving anterolingually along the anterior tooth margin, connecting to the anterobuccal base of the protoconid, this connection slightly more lingual in QMF30488 and slightly more buccal in QMF30489. Postprotostylid cristid extending towards the lingual margin, terminating at the anterior base of the hypoconid; less developed in QMF30488 and QMF30494, fading into the posterior base of the protostylid. Well-developed posterolingually developed crest extending from the protostylid apex, terminating at the posterior end of the longitudinal crevice separating the protostylid and protoconid, more crescentic and with an additional short lingual ridge extending from the protostylid apex in QMF30488. Preentocristid extending anterobuccally (as opposed to anterolingually in other phascolarctids) into the transverse valley separating talonid from trigonid. A second crest extending anterobuccally from the entoconid apex, running parallel to the preentocristid. An additional buccally directed crest extending from the entoconid apex into the valley separating the bases of the entoconid and entostylid ridge. Postentocristid extending posteriorly along the lingual margin to a poorly developed entostylid at the posterolingual corner of the tooth. Large cuspsate ridge in the longitudinal valley between the entoconid and hypoconid analogous to, although more strongly developed than, the entostylid ridge in *Litokoala* and *Phascolarctos*. Entostylid ridge bifurcating anteriorly; two anterobuccally directed ridges extending from its apex, meeting the cristid obliqua. Bifurcating posteriorly; two posterolingually directed ridges terminating at the base of the posterior cingulum. Entostylid not bifurcate in QMF30494.

M_{2-3} . M_2 and M_3 similar to M_1 except for:

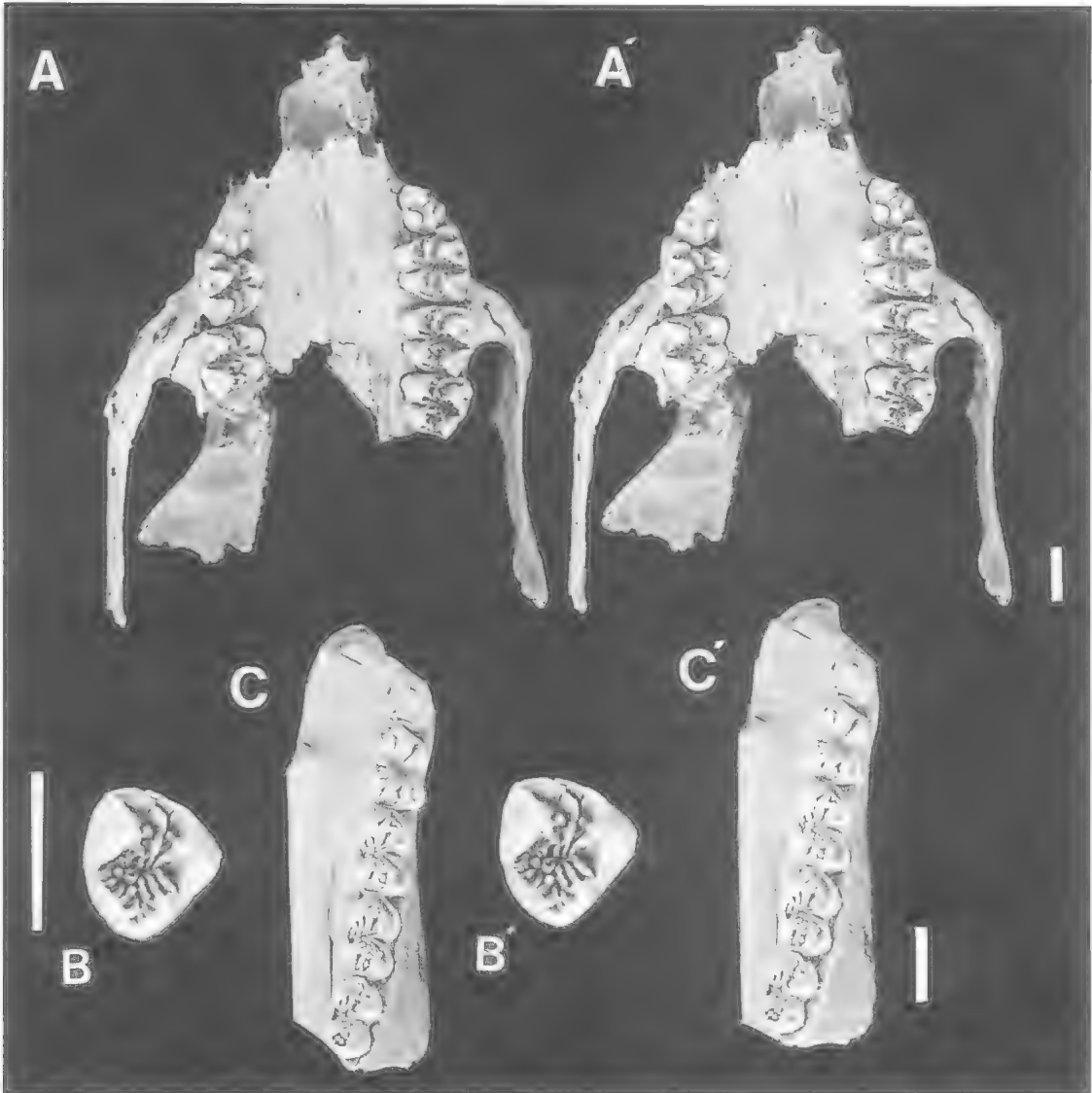


FIG. 2. *Nimiokoala greystanesi* gen. et sp. nov. A-A', QMF30482, holotype, occlusal stereopair of rostral region. B-B', QMF23027, right M⁴, occlusal stereopair. C-C', QMF30487, right dentary fragment, occlusal stereopair. Bar = 5mm.

protostylid absent; paraconid absent; preproto-cristid continuous with anterior cingulum; postprotocristid linear, extending posterolingu-ally towards its junction with the cristid obliqua; premetacristid more prominent, continuous with the anterior cingulum; entostylid reduced result- ing in a more rounded posterolingual tooth cor- ner; entostylid ridge reduced, not bifurcate; entoconid reduced in M₃; hypoconid reduced; preentocristid and posterobuccal metacristid joining, closing the transverse valley well buccal

to the lingual tooth margin. A neomorphic cuspid in the longitudinal valley between the metaconid and protoconid in M₂₋₄, with a well-developed posterolingu-ally directed ridge and a weaker anterobuccally directed ridge extending from its apex, more strongly developed and more sepa- rated from the metaconid in M₂₋₄ of QMF30487 than of QMF30493.

M₄. M₄ similar to M₂₋₃ except for; entostylid ridge further reduced, connecting posteriorly to the posterior cingulum; neomorphic cuspid re-

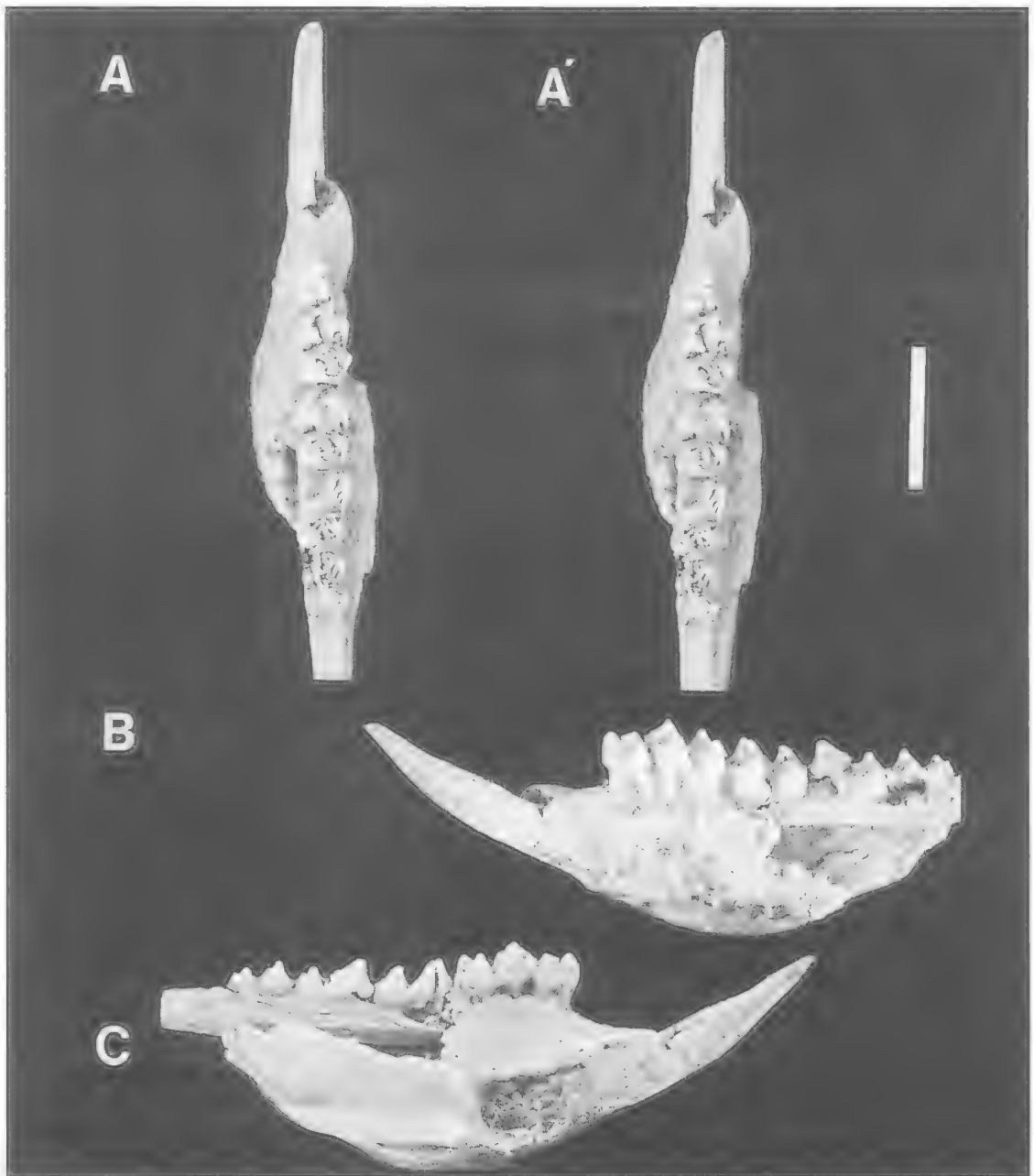


FIG. 3. *Nimiokoala greystanesi* gen. et sp. nov. A-C, QMF30493. A-A', occlusal stereopair of left dentary. B, buccal view. C, lingual view. Bar = 10mm.

duced; postprotocristid and cristid obliqua not meeting end to end but parallel each other (as in *L. kanunkaensis* and some *P. cinereus*); talonid severely reduced resulting in a greater anterior displacement of the entoconid and metaconid

(relative to the hypoconid and protoconid, respectively) (as in *L. kanunkaensis* and some pseudocheirids).

REMARKS. QMF30482 (Fig. 2A) was chosen as

TABLE 1. Dentition measurements (mm) for *Nimiokoala greystanesi* sp. nov. and *Nimiokoala* sp. (last line SAMP19952 only). L=length; W=width; AW, anterior width; PW, posterior width; *=estimate.

A. UPPER CHEEK DENTITION															
Spec.	Side	P3		M1			M2			M3			M4		
		L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
QMF30482 Holotype	L	4.50	3.98	6.45	5.94	5.66	6.05	6.18	5.52	5.70	5.67	4.63			
	R	4.48	3.51	5.99	5.74	5.35	5.92	5.90	5.54						
QMF30483	L	4.51	3.95	-	5.39	-									
	R	4.63	3.83	6.30	5.47	5.68									
QMF30484	R						5.53*	5.63	5.22	5.16	5.15	4.46	4.60	4.48	2.12
QMF30490	L	4.87	4.15												
QMF30495	L	4.52	3.68												
QMF30496	L	4.46	3.53												
QMF30512	L			6.81	5.99	5.93									
QMF24267	R						6.12	6.14	5.41						
QMF24232	L						6.16	6.01	5.42						
QMF30485	L						-	-	5.23						
QMF30498	L						5.18	5.27	4.85						
QMF23026	R						5.67	5.88	5.52						
QMF30497	R									5.28	5.28	4.72			
QMF24233	L												4.12*	3.96	1.91
QMF23027	L												4.47	4.24	2.65
	R												4.67	4.32	2.62
QMF20901	L												4.68	4.69	2.81
	R												4.29	4.16	2.30
B. LOWER CHEEK DENTITION															
QMF30487	R	4.10	3.00	5.70	3.15	3.69	5.77	3.28	3.62	5.56	3.19	3.28	5.07	3.16	3.00
QMF30493	L	3.35	2.44	5.95	3.54	3.40	5.85	3.40	3.43	5.50	-	3.04	5.10		
QMF30494	L	3.60	2.46	5.37	-	3.41	5.86	3.22	3.28	5.57	3.17	3.05			
QMF29624	L	3.86	2.54	5.91	3.07	3.48	5.75	3.26	3.34	5.53	3.30	3.12			
QMF24351	R	3.21	2.25												
QMF24266	R			6.22	3.29	3.66									
QMF30488	R			6.19	3.42	3.66									
QMF30489	R			5.96	3.45	4.04									
QMF20903	L						6.31	3.55	3.92						
QMF24265	R						5.84	3.27	3.30						
SAMP19952	L						5.04	2.77	3.00	5.18	2.95	2.88	4.32	2.53	2.19

holotype because it contains most of the upper dentition well-preserved and relatively unworn. The holotype is thought to represent a juvenile because of the shorter premaxilla in comparison with the adult skull, QMF30483.

***Nimiokoala* sp.**
(Fig. 4, Table 1)

MATERIAL. SAMP19952 left dentary with alveoli of P3 and M1, M2-4 intact from late Oligocene to middle

Miocene South Prospect B locality, Lake Namba, Frome Downs Station, South Australia.

REMARKS. Enamel is missing from the lingual margins of the metaconids and entoconids and the buccal margins of the protoconids and hypoconids. Features of the M2 are difficult to discern because of extreme wear in that tooth. Only points of difference from *N. greystanesi* are noted here.

Lower molars are proportionately smaller (by approximately 15%) and more rounded, espe-

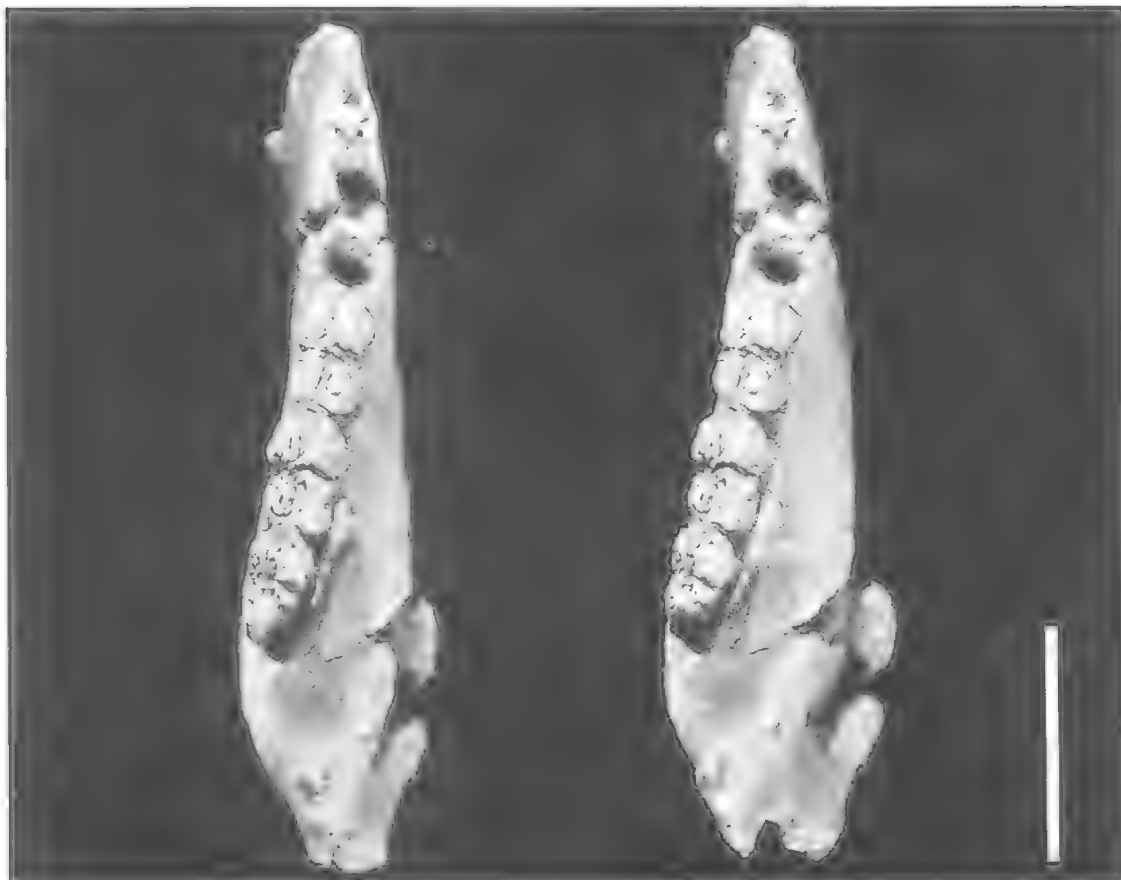


FIG. 4. *Nimiokoala* sp., SAMP19952, from South Prospect B Locality, Lake Namba, South Australia. Occlusal stereopair of right dentary. Bar = 10mm.

cially the talonid. The neomorphic cuspid between the metaconid and protoconid in M_{2-4} is weaker, as is the entostylid ridge. The lingual surfaces of the protoconid and metaconid slope more lingually. The talonid of M_4 is further reduced.

This taxon is left in open nomenclature in the absence of the upper dentition. The features mentioned above as differences between the central Australian and Riversleigh materials vary significantly between individuals of *N. greystanesi* and may not be reliable species indicators.

Litokoala Stirton, 1967

TYPE SPECIES. *Litokoala kutjamarpensisi* Stirton, 1967.

OTHER SPECIES. *Litokoala kanunkaensis* Springer, 1987.

DIAGNOSIS. *Litokoala* differs from other phascolarctids in having a posterobuccal crest extending from the apex of the metaconid on M_{2-4} (although this crest is reduced on M_4); a well-developed posterolingually directed crest from the protoconid apex of M_4 . *Litokoala* differs from other phascolarctids except *Phascolarctos* and *Cundokoala yorkensis* in: having a neomorphic cusplule at the anterior base of the metaconule of M^1 ; an anterolingual protocone crest on M^1 and consequently a much squarer anterolingual margin of that tooth; a metastylid fold wherein the postmetastylid cristid is continuous with the preentocristid; an anteriorly bifurcate preentocristid on the lower molars; and internal ribs on the metaconid and hypoconid of M_1 .

Litokoala differs from all other phascolarctids except *Nimiokoala* in having: a well-developed crescentic paraconule and neometaconule on upper molars; an anteriorly displaced entoconid

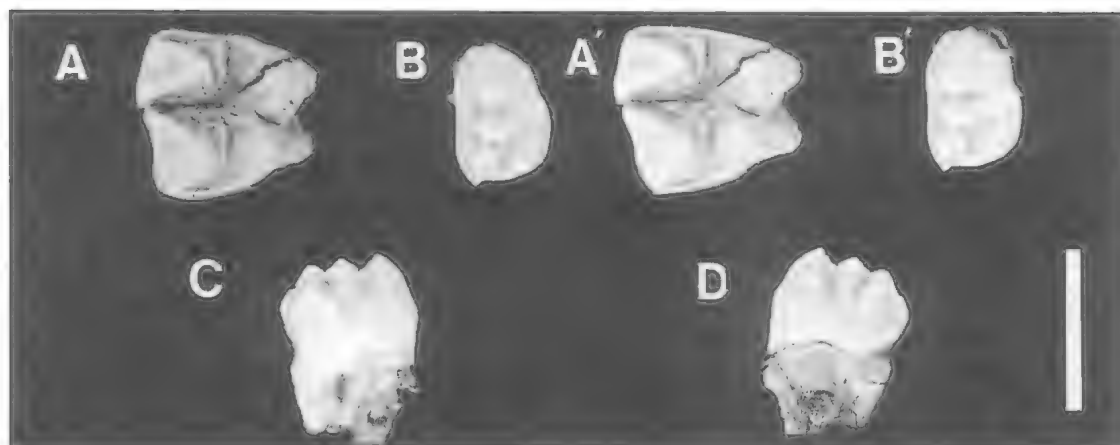


FIG. 5. *Litokoala kanunkaensis*, Henk's Hollow Site, Riversleigh Station. A-A', QMF30502, RM³ occlusal stereopair. B-B', QMF30500, RP³. B-B', occlusal stereopair. C, buccal view. D, lingual view. Bar = 5mm.

(relative to the hypoconid) on M₄; an anteriorly displaced metaconid (relative to the protoconid) on M₄; and a parallel arrangement of the postprotocristid and cristid obliqua on M₄ wherein these cristids do not meet end to end.

Litokoala differs from *Koobor* in: being smaller; having less rounded bases of the paracone, metacone, protocone and metaconule; having less elongate molar proportions; reduced styler cusps; a paraconule on M³; and a neometaconule on M^{1,3}.

Litokoala differs from *Madakoala* and *Perikoala* in: being smaller; higher crowned; more selenodont; having a larger neometaconule; a more crescentic, less linear paraconule; an entostylid ridge in the lower molars; a more lingual junction of the cristid obliqua and postprotocristid; a larger developed protostylid and a more lingual protoconid on M₁; a less strongly developed, more buccally positioned paraconid on M₁; and a more strongly developed entostylid.

Litokoala differs from *Perikoala* in: lacking the well-developed styler border of the paracone and metacone; lacking the additional styler cusp anterior to styler cusp E; having a weaker entoconid lingual shelf; and a weaker premetacristid.

Litokoala kutjampensis differs from *Madakoala* and *Perikoala* in having a buccal extension of the paraconule which connects to the buccal margin of M¹. *Litokoala kanunkaensis* differs from *Madakoala* and *Perikoala* in: lacking the M₂ protostylid ridge; having a less elongate P₃; a more prominent posterobuccal cusp;

and having 3 apices on the longitudinal crest (4 in *Madakoala devisi*; 5 in *M. wellsii*) on P₃.

Litokoala differs from *Nimiokoala* in: having less steeply (more buccally) sloping buccal surfaces of the paracone and metacone; lacking the division of the neometaconule in the more posterior molars; lacking the well-developed posterobuccal crest from the apex of the metaconule; having a weaker posterobuccal crest from the protocone apex; lacking the posterolingual ridge off the apex of the protostylid on M₁; having a less cuspsate, more posteriorly positioned entostylid ridge; having an anterolingually (as opposed to anterobuccally) directed preentocristid; a more posterolingually directed postprotostylid cristid; a lingual entoconid shelf; and a more strongly developed entostylid. *Litokoala kanunkaensis* differs from species of *Nimiokoala* in: lacking the posterolingual cusp on P₃; in having a weaker anterior cusp on P₃; buccal and lingual ribs which extend from the main apices of the longitudinal crest in the P₃; and in lacking the neomorphic cuspid between the metaconid and protoconid of M₂₋₄.

Litokoala differs from *Phascolarctos* and *Cundokoala yorkensis* in: being smaller; having well-developed anterolingual metacristae; having proportionately less elongate lower molars; a less pronounced entoconid basal shelf; and in lacking the ridge connecting the buccal bases of the protoconid and hypoconid of M₂₋₄.

***Litokoala kanunkaensis* Springer, 1987**
(Figs 5-6, Table 2)

MATERIAL. Holotype SAMP32397 (=UCR21926) a right M₂ from latest Oligocene UCR Locality RV-8453 Kanunka North Local Fauna, Etadunna Formation, west side of Lake Kanunka, South Australia. Other material: from Kanunka North Site: UCR21945, a right M₄; UCR21980, a metacone of a right M₃; UCR21979, a metacone of LM¹; late Oligocene. From Henk's Hollow Local Fauna: QMF30500, right P₃; QMF13079, right dentary fragment with posterior half of P₃, M₁₋₂; QMF30502, right M₃; from Gag Site: QMF30501, right M₁; from Gotham Site: QMF30503, M^x fragment containing paracone and buccal half of protocone. From JC9 Site: QMF20809, right M₃; System C, Riversleigh, middle Miocene (Archer et al., 1989; 1991).

DIAGNOSIS. *Litokoala kanunkaensis* differs from *L. kutjampensis* in: having a short longitudinal spur connecting the paracone to the anterior cingulum; lacking the bulbous cuspule at the anterolingual base of the metacone; lacking the protostyle (the latter two features may be result of differences along the tooth row rather than interspecific differences); lacking the distinct posterolingual and anterolingual paracrista; having a strong anterobuccal crest from the metacone apex.

COMPARISON WITH THE HOLOTYPE. Prior to this study *L. kanunkaensis* was known from two isolated lower molars, an M₂ and M₄. Referral of the Riversleigh material to *L. kanunkaensis* is based on the similarity of the M₂ of QMF13079 to the holotype. Some small differences are: M₂ of QMF13079 is slightly larger; posterobuccal metaconid strut is poorly defined and bifurcates in the trigonid longitudinal valley, one spur fading

ing buccally into the protoconid base and the other spur continuing posteriorly then turning sharply lingually before becoming part of the molar crenulation pattern; the entostylid ridge is less cusped and arises from the posterobuccal base of the entoconid (unlike the holotype in which it arises from the postentocristid); and the transverse median valley, the posterior base of the protoconid, the cristid obliqua and the transverse valley separating the bases of the protoconid and hypoconid are more crenulated than in the holotype.

QMF13079 M₂ is significantly more worn than the holotype which may account for the poorer crest definition. Analysis of intraspecific variation in *Phascolarctos cinereus* and *Nimiokoala greystanesi* indicate that these differences do not warrant specific distinction. Most variable features in the modern species include: molar size; pattern and degree of molar crenulations; cristid obliqua; entostylid ridge. Although the entostylid ridge may be phylogenetically significant in phascolarctids, it is highly variable. It may be a well-developed cusped structure, relatively indistinguishable as a series of discontinuous crenulate ridges, completely isolated at the base of the entoconid or variably connected to the postentocristid, the base of the entoconid or the posterior cingulum. Hence differences between the holotype and QMF13079 are within intraspecific variation.

DESCRIPTION. P₃ (Fig. 5B-D). Short, semi-rectangular, of 4 major cusps anteriorly, medially, posteriorly and posterobuccally on the crown. Anterior, medial and posterior cusps on a longitudinal crest extending the length of the crown. Anterior cusp tallest, 1/3 of way along longitudinal crest, above the anterior root of P₃. Anterior, buccal and lingual crests extending from its apex; anterior crest fading into the anterolingual base of the crown; lingual crest fading down the lingual tooth margin, curving posterolingually at its tip; buccal crest short, fading into the buccal tooth margin. Anterobuccal, anterolingual and posterolingual crests extending from the posterior cusp apex; anterobuccal crest poorly developed, extending into the valley between the posterior and posterobuccal cusps, meeting a short lingual ridge from the posterobuccal cusp apex; anterolingual crest better developed, fading down the lingual margin; posterolingual crest curving anterolingually along the base of the crown, becoming cingulum-like, fading into the base of the posterior cusp. Posterobuccal cusp

TABLE 2. Measurements (mm) for right lower dentition of *Litokoala kanunkaensis* from Riversleigh's System C deposits. Abbreviations as for Table 1.

QMF No.	P ₃		M ₁			M ₂			M ₃		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW
30500	4.12	3.10									
30501			4.72	2.63	3.04						
13079		2.62	4.89	3.14	3.58	5.15	3.43	3.57			
20809									5.48	3.39	3.40

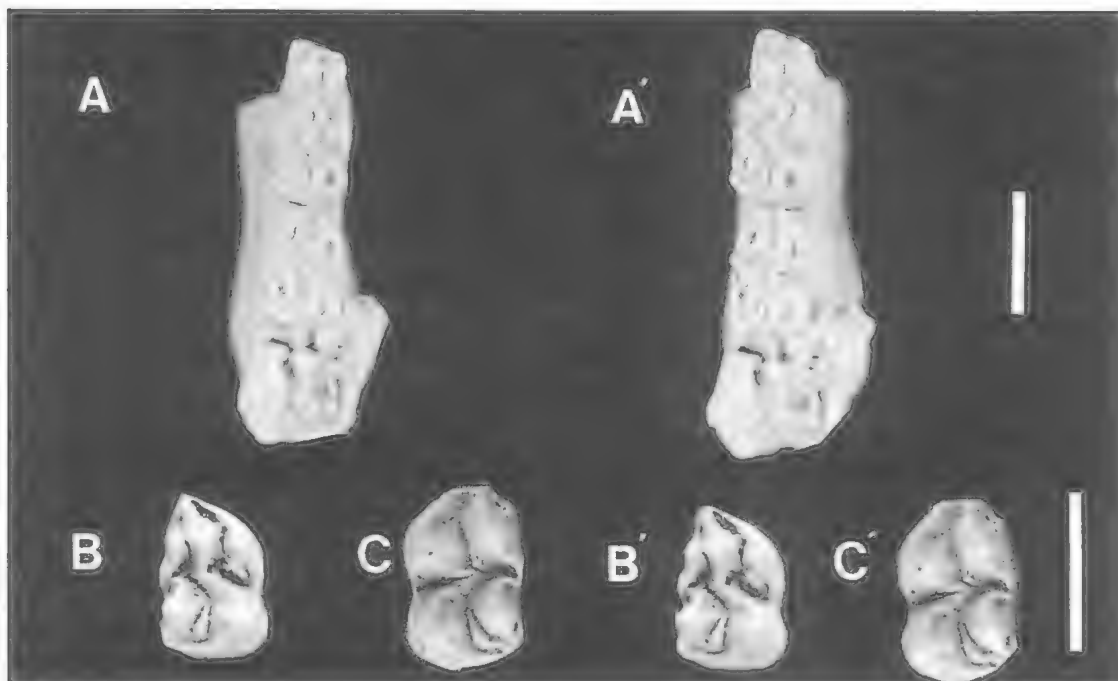


FIG. 6. *Litokoala kanunkaensis*. A-A', QMF13079, right dentary fragment with posterior half of P₃, M₁₋₂, occlusal stereopair. B-B', QMF30501, RM₁, occlusal stereopair. C-C', QMF20809, LM₃ occlusal stereopair. Bar = 5mm.

opposite but slightly posterior to the posterior cusp, with a short posterolingual ridge extending from its apex and terminating at the posterior end of the valley between the posterior and posterobuccal cusps, with short, anterobuccal crest extending from its apex and fading towards the base of the crown.

M₁ (Fig. 6B). Semi-rectangular, tapering slightly anteriorly. Protoconid most worn of the major cusps, with well-developed protostylid opposite but slightly posterior to apex. Short, linear cristid extending posteriorly from the apex of the protostylid into the transverse valley, bifurcating into posterolingual and posterobuccal arms, both arms terminating in the transverse valley between the talonid and trigonid. (In QMF13079 postprotostylid cristid more crenulated, bifurcation less distinct and more a part of the crenulation pattern). Anterolingual cristid from protostylid apex crescentic, well defined, continuous with the anterior cingulum extending to the anterolingual corner of the tooth. Lingual rib from the protostylid apex short, fading into its base. Crescentic, cingulum-like ridge extending posterobuccally from the posterobuccal base of the protostylid, fading into the anterior base of the

hypoconid. Preprotocristid extending anterolingually to the paraconid, a moderately developed, slightly cusped structure at the anterolingual tooth corner, with a posterolingually directed ridge fading down the lingual margin towards the base of the crown. Anterobuccal crest continuous with the anterior cingulum/preprotostylid cristid. Postprotocristid extending posteriorly meeting cristid obliqua slightly lingual to the longitudinal axis of the tooth. Postmetacristid extending posterolingually from the apex of the metaconid to the lingual margin, swelling at this point to form the metastylid. Posterolingual ridge from the metastylid short, fading down the lingual tooth margin, better developed in QMF13079. Postmetastylid cristid a short, buccal ridge, continuous with the prentocristid, resulting in the metastylid fold. Entoconid sub-pyramidal. Preentocristid extending anteriorly towards the transverse axis, curving lingually, bifurcating with one spur extending lingually to meet the postmetastylid cristid and other extending anterobuccally into the transverse valley to lingual base of the junction of the postprotocristid and cristid obliqua. QMF13079 (Fig. 6A-A') with a short anterolingual spur ex-

tending from the junction of the postprotoeristid and cristid obliqua to the anterobuccal spur of the preentocristid. A well-developed anterobuccal ridge extending from the entoconid apex, terminating at the anterobuccal base of the entoconid, just lingual to the anterior arm of the entostylid ridge. Postentocristid curving posterolingually from the entoconid apex to the posterolingual tooth corner, swelling at this point to form a small entostylid. A short anterolingual ridge fading down the lingual tooth margin from the entostylid apex, better developed in QMF13079. A short posterobuccal ridge extending from the entostylid apex, continuous with the posterior cingulum. Well-developed cusped entostylid ridge at the posterobuccal base of the protoconid, fading anteriorly along the longitudinal tooth axis, with a shorter posterior spur terminating before meeting the posterior cingulum. QMF13079 with entostylid ridge extending buccally from the postentocristid, similar in this respect to the holotype. Hypoconid largest of the main cusps. Posthypocristid extending posterolingually along the posterior tooth margin, becoming continuous with the posterior cingulum. Cristid obliqua long, well-developed, crenulated, relatively linear, extending anterolingually from the hypoconid apex, meeting the postprotoeristid on the transverse valley slightly lingual to the longitudinal axis. Talonid basin, transverse valley between the talonid and trigonid and buccal base of the entoconid and protoconid crenulated. Lingual base of the hypoconid and protostylid lightly crenulated. Protostylid occupying the anterobuccal corner of the tooth, lying well buccal to the longitudinal axis. Short lingual ribs extending from apices of the entoconid, hypoconid, protoconid and protostylid. Short buccal ribs off the protoconid and metaconid apices, less prominent in the holotype.

M₃ (Fig. 6C-C') is similar to the holotype except for: being slightly larger, having buccal bases of the protoconid and hypoconid more rounded, the lingual shelf of the metaconid better developed, the cristid obliqua and postprotoeristid meeting at a more lingual position, the anterobuccal entoconid ridge and the posterobuccal metaconid ridge poorly developed (possibly due to wear) and the entostylid ridge extending buccally from the postentostylid cristid rather than from the postentocristid.

M³ (Fig. 5A-A'). Length 5.16mm; anterior width 5.22mm; posterior width 4.28mm. Subquadrate, tapering slightly posteriorly, with shallow surface enamel crenulations in the transverse

valley and posterior base of paracone. Buccal bases of the protocone and metacone large, rounded, with lingual bases of all major cusps sloping gently lingually. Triangular buccal surface of paracone reduced relative to the metacone (less marked in QMF30503). Buccal margin of the paracone sloping anterolingually; buccal margin of the metacone sloping slightly posterolingually in occlusal view. Buccal basins of the paracone and metacone shallow and open. Buccal basin of the paracone deeper than that of the metacone. Styral cusps B and C well-developed on the paracone. Styral cusps on the metacone poorly developed, styral decrease progressively from B to E. In QMF30503 styral cusp C more strongly developed, almost closing the paracone buccal basin. Preparaerista relatively short crest, extending anterobuccally to the anterobuccal tooth corner, bifurcating, with one arm curving buccally and becoming continuous with the anterior cingulum, the other short ridge extending posterobuccally, fading along the paracone buccal margin to a slight swelling representing styral cusp B. Longer, relatively linear postparaerista extending posterobuccally to the buccal margin, meeting premetaerista, closing the buccal exit of the transverse valley. Styral cusp D a slight swelling at the buccal tip of the premetaerista. Postmetaerista linear, extending posterobuccally from the metacone apex to the posterobuccal tooth corner, meeting the posterior cingulum. Paraconule at the anterolingual base of the paracone, slightly cusped at this point, bifurcating anteriorly, with main linear arm extending anterobuccally, terminating at the anterolingual base of the paracone before meeting the anterior cingulum, with a minor arm connecting the anterior cingulum. Linear posterior arm of the paraconule extending posteriorly along the longitudinal valley between the paracone and protocone, bifurcating at a point just anterior to the transverse median valley. A short posterobuccal arm meeting the posterolingual paraerista; second arm continuing posteriorly into the transverse median valley. A cusped, anteriorly bifurcate neometaconule at the anterolingual base of the metacone, with the main crenulated arm extending anterobuccally, meeting the anterolingual metaerista at the base of the metacone. A shorter arm fading lingually from the neometaconule apex into the longitudinal valley at the buccal base of the hypocone. Posteriorly, the linear arm of the neometaconule fading into the longitudinal valley between the metacone and metaconule. Buccal surfaces of the protocone and

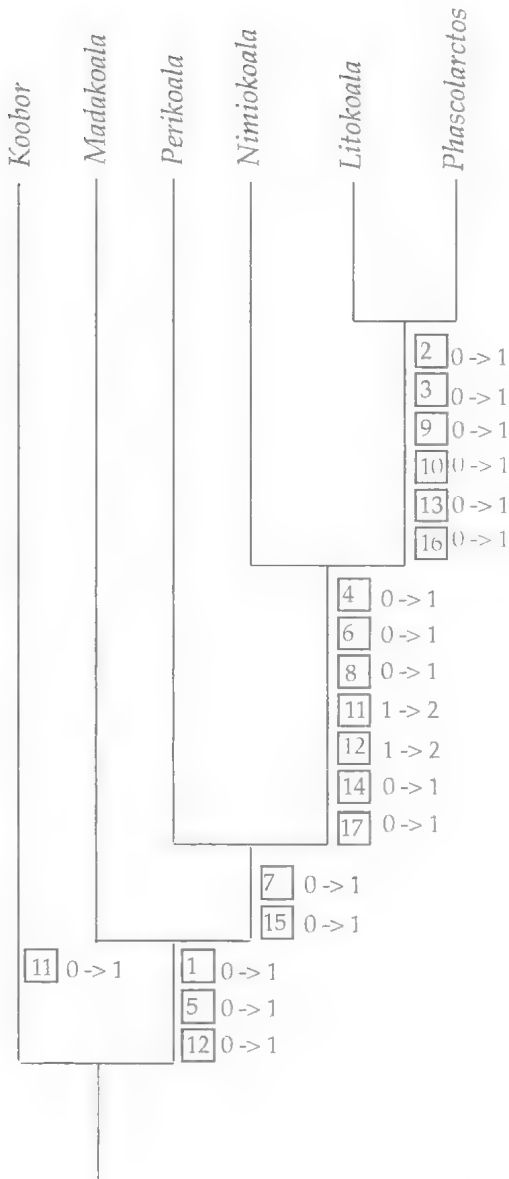


FIG. 7. Phylogeny of the Phascolarctidae based on cladistic analysis of dental characters (Table 3). Apomorphies are represented by boxed numbers. Arrows indicate character state transformations. 0 = plesiomorphic character state; 1 = derived character state; 2 = most derived character state.

metaconule sloping gently buccally. Preprotocrista long, crescentic crest, extending anterobuccally, curving more buccally into the longitudinal valley, meeting the anterior spur off the paraconule, becoming continuous with the

anterior cingulum. The slightly more crescentic postprotocrista extending posterobuccally toward the transverse valley, turning sharply buccally, meeting the short, slightly crescentic prehypocrista at the buccal end of the transverse valley between the metaconule and protocone. Prehypocrista bifurcating just posterior to the transverse valley, with one arm continuing anterobuccally to the postprotocrista, with the other crenulated arm extending buccally, then anterobuccally into the transverse median valley. Junction of the postprotocrista and prehypocrista effectively sealing off the lingual exit of the transverse valley well-in from the lingual margin. Two short ridges at the posterolingual base of the protocone and the anterolingual base of the metaconule. Posterolingual base of the protocone slightly crenulated and cingulum-like. The long, slightly crescentic posthypocrista extending posterobuccally, becoming continuous with the posterior cingulum. A relatively well-developed anterobuccal ridge from the metaconule apex, fading towards its base. Posterobuccally directed ridge from the protocone apex fading into the posterobuccal base of the protocone. Posterolingual paracrista bifurcating at its base, one arm meeting the anterobuccal arm of the paraconule and continuing into the transverse median valley, with the other extending posterobuccally into the transverse median valley. Anterolingual metacrista bifurcating at the anterolingual base of the metacone, one arm continuing anterolingually to meet the anterobuccal arm of the neometaconule, the other extending anterobuccally into the transverse valley between the paracone and metacone.

PHYLOGENETIC ANALYSIS

Seventeen dental characters which provide phylogenetically useful data on phascolarctid relationships are analysed (Tables 3, 4). Character polarities were determined using selenodont ilardiids and subselenodont wynyardiids as outgroups.

CHARACTER ANALYSIS

Thirty potentially useful dental characters were reduced to 17 following analysis of variation in the living species. The Pleistocene *Cundokoala yorkensis* Pledge, 1992 is not significantly different in dental morphology from *Phascolarctos*; generic distinction is not warranted. It is here regarded as a separate species of *Phascolarctos*.

TABLE 3. A list of character state polarities (PLES= plesiomorphic state; APO= apomorphic state) for the Phascolarctidae using ilariids and wynyardiids (Marsupialia: Vombatiformia) as outgroups. A=absent; P=present; LI=linear; C=crescentic; LA=large; R=reduced; W=weak; S=small; M=moderate; B=buccal; LIN=lingual third of trigonid

CHARACTER	PLES	APO
1. Bladed premolar	A	P
2. Trenchant premolar	A	P
3. Posterobuccal cusp on P ³	P	A
4. Structure of paraconule	LI	C
5. Development of neometaconule	A	P
6. Protostyle development	A	P
7. Styler cusp development	LA	R
8. Posterolingual paracristae	A/W	P
9. Neomorphic cuspule at base of metaconule	A	P
10. Anterolingual protocone crest	A	P
11. Parastyle development on M ¹	S	M/L
12. Protostylid development on M ₁	A	P
13. Metastylid fold	A	P
14. Entostylid ridge	A	P
15. Position of protoconid on M ₁	B	LIN
16. Buccal ribs on lower molars	A	P
17. Anteriorly displaced entoconid relative to hypoconid and anteriorly displaced metaconid relative to protoconid in M ₄	A	P

1. *Premolar cusp pattern*: P³ in most phascolarctids (e.g. *Madakoala*, *Perikoala*, *Nimiokoala*, *Litokoala*, *Phascolarctos*) has a tendency to be bladed, as opposed to bicusped and weakly bladed in *Koobor*. Woodburne et al. (1987a) regard the bicusped P³ as plesiomorphic among phascolarctids but its occurrence in other vombatiform groups (e.g. ilariids and wynyardiids) suggests that it is apomorphic in phascolarctids.

2. *Trenchant P³*: *Phascolarctos* has a trenchant

P³ in contrast to a bulbous P³ in *Koobor*, *Madakoala*, *Perikoala* and *Nimiokoala*. Ilariids and wynyardiids have a bulbous, non-trenchant P³ suggesting the trenchant P³ in *Phascolarctos* is apomorphic.

3. *Posterobuccal cusp of P³*: The small posterobuccal cusp on P³ in *Koobor*, *Madakoala*, *Perikoala* and *Nimiokoala* is lacking in *Phascolarctos*. It is absent in wynyardiids and variable in ilariids. Its occurrence in most phascolarctids and ilariids suggests that it is plesiomorphic among phascolarctids.

4. *Crescentic paraconule*: The paraconule varies among phascolarctids from a small, linear structure in *Madakoala* and *Perikoala* to moderately developed in *Phascolarctos* (although not uniform), to a large crescentic paraconule in *Litokoala* and *Nimiokoala* occupying the longitudinal valley between the paracone and protocone. It is a moderate swelling at the anterolingual base of the paracone in M¹ of *Koobor*; however, it is suppressed on M²⁻³ as in ilariids. A paraconule is absent in wynyardiids but a small swelling at the anterolingual base of the paracone in ilariids. Hence, absence of a crescentic paraconule is regarded as plesiomorphic among phascolarctids.

5. *Neometaconule*: Absent in *Koobor*, weakly developed (or absent) in *Madakoala* and *Perikoala*, variable in *Phascolarctos*, large and crescentic in *Litokoala* and *Nimiokoala* (although reduced in the more posterior molars) and double cusped in the latter. Its absence is regarded as plesiomorphic in koalas because of its absence in ilariids and wynyardiids.

6. *Protostyle*: Present in *Phascolarctos*, *Nimiokoala* and *Litokoala* although it generally diminishes in size from M¹ to M⁴. It is absent in *Madakoala*, *Perikoala*, *Koobor*, ilariids and wynyardiids which suggests its presence is apomorphic.

7. *Stylar cusp development*: Large stylar cusps are thought to be primitive among

TABLE 4. Character state distribution within Phascolarctidae. Abbreviations: 0, plesiomorphic state; 1, apomorphic state; 2, more derived apomorphic state; ?, signifies missing data.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Phascolarctos</i>	1	1	1	0	1	1	1	1	1	1	1	2	1	1	1	1	0
<i>Litokoala</i>	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1
<i>Nimiokoala</i>	1	0	0	1	1	1	1	1	0	0	2	2	0	1	1	0	1
<i>Perikoala</i>	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	0
<i>Madakoala</i>	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
<i>Koobor</i>	0	0	0	0	0	0	0	0	0	0	1	?	?	?	?	?	?

diprotodontians (Rich & Archer, 1979), reflected in the enlarged styler cusps of ilariids and wynyardiids. Large styler cusps occur in *Koobor* and *Madakoala*. Although *Perikoala* has reduced styler cusps, the styler region is represented by a longitudinal crest that appears to subsume relatively large styler cusps. Those of *Nimiokoala*, *Litokoala* and *Phascolarctos* (excluding the parastyle of M^1) are suppressed relative to all other phascolarctids. Because of the large styler cusps in ilariids and wynyardiids, reduction in some phascolarctids is regarded as apomorphic.

8. *Posterolingual paracristae*: Well-developed and aligned with the preparacristae in *Nimiokoala*, *Litokoala* and *Phascolarctos* but absent (or weakly expressed) in *Koobor*, *Madakoala*, *Perikoala*, ilariids and wynyardiids. Absence is regarded as plesiomorphic.

9. *Cuspule at the anterolingual metaconular base of M^1* : A bulbous cuspule lies at the anterolingual base of the metaconule on M^1 of *L. kutjamarpenis* (M^2 - 4 unknown). It is variable in *Phascolarctos* but is absent in all other phascolarctids and ilariids and wynyardiids suggesting that absence is plesiomorphic.

10. *Anterolingual protocone crest of M^1* : An anterolingual crest extends from the apex of the protocone towards the base of the crown on M^1 of *L. kutjamarpenis* and *Phascolarctos* resulting in a relatively square protocone base. This crest is absent in all other phascolarctids, in wynyardiids and in ilariids. Absence is regarded as plesiomorphic among phascolarctids.

11. *Parastylar development on M^1* : The parastyle ('styler cusp A') is regarded as a separate character (distinct from character 7) because it undergoes independent evolutionary change relative to styler cusps B through E. Small on M^1 of *Madakoala* and *Perikoala*; moderately developed in *Koobor*, *Litokoala* and *Phascolarctos*; large in *Nimiokoala*. The small parastyle of ilariids and wynyardiids suggests that this is the plesiomorphic condition.

12. *Protostylid*: The protostylid on M^1 has developed independently in pseudocheirids (Woodburne et al., 1987b), macropodoids (Archer, 1978a) and ilariids (Tedford & Woodburne, 1987). In koalas, the protostylid ranges from weak (*Madakoala*, *Perikoala*) to very large (*Nimiokoala*, *Litokoala*, *Phascolarctos*). Lower molars of *Koobor* are unknown. Because a protostylid is absent in wynyardiids (Pledge, 1987a) and probably ilariids (Tedford & Woodburne, 1987 consider both alternatives), a protostylid is interpreted here as derived.

13. *Metastylid fold*: An autapomorphy of the Phascolarctidae. *Phascolarctos* and *Litokoala* have a metastylid fold in which the post-metastylid cristid is continuous with the pre-entocristid. *Perikoala* and *Madakoala* lack the metastylid fold which is represented by a swelling at the posterior tip of the postmetacristid. *Nimiokoala* lacks a metastylid fold and the metastylid is reduced relative to other phascolarctids. Because it is absent in ilariids and wynyardiids it is difficult to determine polarity. However, considering that discrete metaconids and entoconids is the plesiomorphic condition in all marsupial groups, the condition within the Phascolarctidae in which these cusps are linked by blades, in this case via a metastylid, is interpreted as derived.

14. *Entostylid ridge*: Present in *L. kanunkaensis* and *Phascolarctos* and a well-developed cuspid in an homologous position in *Nimiokoala*. Its absence in the lower molars of ilariids and wynyardiids suggests that absence is plesiomorphic.

15. *Position of the protoconid on M^1* : Woodburne et al. (1987a) used this to determine koala intrafamilial relationships, with the more plesiomorphic koalas having a less lingual protoconid because of weaker protostylid development. The protoconid is within the lingual third of the trigonid of M^1 in *Perikoala*, *Nimiokoala*, *Litokoala* and *Phascolarctos*. Considering the buccal protoconid in wynyardiids and ilariids, the more lingual position in some phascolarctids is considered to be derived.

16. *Ribs on the conids of lower molars*: Internal ribs on the protostylid, metaconid, protoconid, entoconid and hypoconid of lower molars is apomorphic and shared by *Litokoala* and *Phascolarctos*. These ribs are absent in all other koalas. Presence is considered derived.

17. *Anteriorly displaced entoconid and anteriorly displaced metaconid of M^4* : Torsion of M^4 such that the entoconid is displaced anteriorly relative to the hypoconid and the metaconid is displaced anteriorly relative to the protoconid occurs in *Litokoala* and *Nimiokoala* but no other phascolarctids. This condition is absent in ilariids and wynyardiids; absence is interpreted plesiomorphic.

RESULTS

Wagner analysis using the branch and bound algorithm produced a single most parsimonious tree involving 22 steps with a CI of 0.864 and a RC of 0.746 (FIG. 7).

DISCUSSION

Recent classifications (e.g. Woodburne, 1984; Aplin & Archer, 1987) group the 6 fossil and living genera (14 species) of koalas in the Phascolaretidae; however, they also predict a large morphological range of koala-like animals. Woodburne (1984) erected the Superfamily Phascolaretoidea and Aplin & Archer (1987) the Infraorder Phascolaretomorphia, each containing only the Phascolaretidae. Complex molar morphology and plesiomorphic basiscranial morphology of *Nimiokoala* indicate a more diverse infraorder of phascolaretomorphians.

In some aspects of dental morphology, *Nimiokoala* appears to have converged on pseudocheirids and ektopodontids. Slight torsion is evident in lower molars of *Nimiokoala* and the consequent arrangement of the metaconid and entoconid is similar to some pseudocheirids (e.g. *Pseudochirops archeri*). Springer (1987) also noted more similarities in the M_4 of *L. kanunkaensis* to pseudocheirids than to any other phascolaretid. This is also the case with the M_4 of *Nimiokoala*.

Well-developed parastyle, large paraconule and large neometaconule of the upper molars of *Nimiokoala* and the entostylid ridge and neomorphic cuspid on the lower molars are reminiscent of the cuspidate loph(id)s of ektopodontid molars; in particular the lower molars of *Darcus duggani* Rich, 1986 from the Pliocene Hamilton Local Fauna, Victoria. Archer (1976) suggested that the ektopodontid molar pattern may have evolved through an alignment of the wrinkles, conules and crenulations in the molars of selenodont forms and in particular, the koalas. The high crowned, highly crenulate, complex molars of *Nimiokoala* support this view.

Recent classifications (Archer & Aplin 1987; Marshall et al., 1989) support an ektopodontid/phalangerid affinity and place the Ektopodontidae within the Phalangerioidea based on the shared strongly angulate cristid obliqua and reduced metaconid on the lower molars and the loss of P1. Consequently, similarities in phascolaretid and ektopodontid molars suggest similar ecological niches. Pledge (1982) suggested several possible dietary preferences of ektopodontids, ranging from browsing and frugivorous to granivorous and insectivorous. Similar dietary specialisations could explain the complex dentitions of *Nimiokoala*.

Since the first fossil koala was described in 1957 there have been two different attempts to

analyse intrafamilial relationships. Archer (1978a) separated phascolaretids into *Litokoala*, *Koobor* and *Perikoala* Phascolaretos lineages. *Litokoala kutjamarpensis* was considered to be the most plesiomorphic phascolaretid based on the metaconule and lingual buttresses on the metacone of the upper molar (Archer, 1978a). *Perikoala* and *Phascolaretos* were interpreted to be more closely related to each other than either was to *L. kutjamarpensis*. However, Archer (1978a) also noted a large structural distance separating these groups. *Perikoala* exhibited a number of plesiomorphic features relative to *Phascolaretos* and several autapomorphic features that precluded it being antecedent to *Phascolaretos*. Molar morphology of *Koobor* led to its interpretation by Archer (1978a) as the sister-group of a combined *Phascolaretos*/*Perikoala* clade.

Woodburne et al.'s (1987a) cladistic analysis followed a reassessment of character state morphoclines for phascolaretids. Relative positions of *Phascolaretos*, *Litokoala*, *Perikoala* and *Mudakoala* are confirmed herein (Fig. 7). Relationships of *Litokoala* have been unclear due to its poor fossil record. Archer (1978a) regarded it as the plesiomorphic sister group of all phascolaretids based on a single upper molar. Re-analysis of that tooth by Woodburne et al. (1987a) and Springer's (1987) 2 isolated lower molars and upper molar fragments of *L. kanunkaensis* suggested *Litokoala* was more closely related to *Phascolaretos*. *Litokoala* material from Riversleigh supports Woodburne et al.'s (1987a) hypothesis.

Features now found to support the *Litokoala* and *Phascolaretos* relationship include the neomorphic cuspid at the anterolingual base of the metaconule on M^1 (and M^{2-4} in *Phascolaretos*), the metastylid fold in which the postmetastylid cristid is a continuous fold with the preentocristid and the internal ribs on the cuspid of lower molars. Features, regarded by Springer (1987) as autapomorphies of *L. kanunkaensis* but which are in fact variably present in *Phascolaretos* include anteriorly bifurcate pre-entocristid, reduced talonid on M_4 and parallel arrangement of the cristid obliqua and postprotocristid on M_4 wherein these cristids do not meet end to end. The latter two features are also variably present in *Nimiokoala*. *Litokoala* is a derived relative to *Phascolaretos* in having a more crescentic paraconule and neometaconule in the upper molars, a well-developed metaconid

posterobuccal crest on M_{2.4} and in having a well-developed posterolingual protoconid on M₁.

Nimiokoala, *Litokoala* and *Phascolaretos* form a clade by sharing a protostyle in the upper molars, strong posterolingual paracristae, a large protostylid on M₁ and a well-developed entostylid ridge. *Litokoala* and *Nimiokoala* are derived relative to *Phascolaretos* in the shared crescentic paraconule and neometaconule in M¹⁻⁴ and a well-developed parastyle on M¹. *Litokoala* and *Nimiokoala* synapomorphies, interpreted as convergences (Fig. 7) are: well-developed, highly crescentic paraconule and neometaconule, large, pyramidal parastyle and extreme torsion on M₁ such that the entoconid and metaconid are displaced anteriorly relative to the hypoconid and protoconid, respectively. *Nimiokoala* is derived relative to other phascolaretids in having strong posterobuccal crests from the apices of the protocone and metaconule, a discontinuous neometaconule which is subdivided into two cusped parts, a posterolingual cuspule on P³, a well-developed posterolingual protostylid cristid on M₁, weak metastylid in the lower molars, an anterobuccally directed preentoconid (anterolingually directed in other phascolaretids) and a neomorphic cuspid occupying the trigonid basin between metaconid and protoconid on M_{2.4}.

There are doubts about the inclusion of *Koobor* in Phascolaretidae. Pledge (1987b) suggested that *Koobor* is allied to ilariids such as *Kuterinjanama*. Figure 7 may support the hypothesis that it lies outside the Phascolaretidae. Clarification of *Koobor*'s relationships requires discovery of lower molars because these differ significantly in ilariids and phascolaretids.

Except for 2 partial skulls from Riversleigh, extinct phascolaretids are represented by isolated teeth or dentitions. As a result, current understanding of the basicranial region is based on the modern species. *Phascolaretos cinereus* has an autapomorphic bilaminar bulla wherein the tympanic cavity is roofed by both an alisphenoid tympanic process and the squamosal epitympanic wing (Aplin, 1987). The partially preserved basicranial region of *Nimiokoala greystanesi* (Fig. 1A-C) exhibits the plesiomorphic diprotodontian condition wherein the alisphenoid forms the roof of the tympanic cavity, suggesting a large structural distance between these koalas. The plesiomorphic basicranium of *N. greystanesi* supports the hypothesis that phascolaretids diverged from near the base of the diprotodontian tree (Archer, 1976).

Intragenetic relationships of *Litokoala* are dif-

ficult to interpret due to a lack of comparable material between the species. *Litokoala kanunkaensis* appears to be plesiomorphic relative to *L. kutjamarpuensis* because it lacks a proto style and the bulbous cuspule at the anterolingual base of the metaconule on M³. However, these features may be a result of changes along the tooth row (ie. an artefact of comparing an M¹ with an M²) rather than interspecific differences.

Litokoala kanunkaensis from early-middle Miocene System C (Archer et al., 1989; 1991) is the same age or slightly younger than, the Kutjamarpu Local Fauna.

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A KINGFISHER (HALCYONIDAE) FROM THE MIOCENE OF RIVERSLEIGH,
NORTHWESTERN QUEENSLAND, WITH COMMENTS ON THE EVOLUTION OF
KINGFISHERS IN AUSTRALO-PAPUA

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A Miocene kingfisher from Riversleigh, northwestern Queensland, represented by a complete carpometacarpus, is the earliest record of the Halcyonidae from Australasia. It shares similarities with several modern genera, but a positive generic identification cannot be made. Although it can be distinguished from extant species, this skeletal element is insufficient to erect a new genus. A processus dentiformis in *Tanysiptera* and *Melidora* and its absence in *Todiramphus* and other genera suggest that the former genera are among the more primitive of the Australo-Papuan kingfishers. The less developed processus dentiformis in the Riversleigh specimen is consistent with it being an earlier member of the *Todiramphus* lineage. Of living kingfishers examined, all that retain the processus dentiformis are inhabitants of rainforest. □ *Kingfisher, Halcyonidae, Riversleigh, Miocene, evolution.*

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The kingfishers (Alcedinidae s.l.) are subdivided into 3 subfamilies. DNA-DNA hybridisation studies (Sibley & Ahlquist, 1990) suggested that these should be recognised as families. Cerylidae do not occur in Australasia. Alcedinidae ('river kingfishers') and Halcyonidae [= Dacelonidae auct.] ('tree kingfishers') are represented in Australo-Papua by 5 species in 1 genus and 21 species in 5-6 genera, respectively (Beehler et al., 1986; Fry et al., 1992; Christidis & Boles, 1994).

There are no named Tertiary forms from outside Australasia (Olson, 1985). Mourer-Chaurviré (1982) listed this family (Alcedinidae s.l.) from Eocene-Oligocene deposits at Quercy, France, and Olson (1985) noted that he had examined specimens close to this family originating from the lower Eocene of North America and the medial Eocene of Germany. All Australian Quaternary kingfisher material is referable to modern taxa: *Alcedo azurea*, *Dacelo novaeguineae*, *Todiramphus pyrrhopygia* and *To. sanctus* (Baird, 1991). No Tertiary kingfishers are known from Australasia (Fordyce, 1991; Vickers-Rich, 1991).

Described herein is a Miocene kingfisher from Riversleigh, northwestern Queensland.

METHODS

Measurements (Steadman, 1980) were made with vernier calipers accurate to 0.05mm and rounded to the nearest 0.1mm. Terminology of

bones largely follows Baumel & Witmer (1993). *Todiramphus* and *Syma* are considered distinct from *Halcyon*, following Christidis & Boles (1994). Institutional prefixes are AM (Australian Museum), ANWC (Australian National Wildlife Collection), MV (Museum of Victoria), QM (Queensland Museum) and USNM (United States National Museum).

SYSTEMATIC PALAEONTOLOGY

Family HALCYONIDAE

Although the Halcyonidae includes some of the largest kingfishers in the world, size is not a valid character for family allocation of osteological material. Australia's 2 Alcedinidae, *Alcedo pusilla* and *A. azurea*, are the country's smallest kingfisher species (wing lengths 55mm and 75mm, respectively), but the closely related *A. websteri* of New Britain has a wing length of 90mm, overlapping in size the smaller halcyonids (e.g., *Todiramphus macleayi*, wing length 90mm).

The carpometacarpus of the Halcyonidae can be distinguished from that of the Alcedinidae and Cerylidae (Table 1) and on this basis the Riversleigh fossil is assigned to the Halcyonidae.

Halcyonid gen. indet.

Fig. 1C

MATERIAL. QMF29719. right carpometacarpus with only minor abrasion to some surfaces from ?middle

TABLE 1. Characters for separating the carpometacarpus of the Alcedinidae, Cerylidae and Halcyonidae.

Character	Alcedinidae	Cerylidae	Halcyonidae
proximal border of dorsal carpal trochlea	more angular	more rounded	more angular
development of os metacarpalis alulare	more gracile	more robust	more robust
orientation of os metacarpalis alulare	more caudal	more caudal	more proximal
tip of processus extensorius	rounded	expanded, slightly rugose	rounded
position of processus intermetacarpalis	more proximal	more proximal	more distal
width and distal extension of sulcus interosseus	narrower, not as extensive distad	broad, extending almost to facies digitalis minor	broad, extending almost to facies digitalis minor
plane of synostosis metacarpalis distalis and distal ends of os metacarpalis major and os metacarpalis minor	os metacarpalis minor depressed below plane	os metacarpalis minor depressed slightly below plane	flat, coplanar

Miocene to early late Miocene Last Minute Site from System C (Archer et al., 1989, 1994). This site is interpreted to represent shallow pools or even emergent accreting surfaces, and is dominated by terrestrial vertebrates including the possums *Djilgaringa gillespieae* Archer et al., 1987 and *Strigocuscus reidi* Flannery & Archer, 1987. Other avian taxa from this site are a range of passerines, including the logrunner *Orthonyx kaldowinyeri* Boles, 1993.

DESCRIPTION. Length 15.8mm. Length of spatium intermetacarpale 61% of length of carpometacarpus. Processus dentiformis low and pointed, located about midway between the distal edge of facies articularis alularis and the cranialmost point of facies articularis digitalis major. Os metacarpale majus of about equal thickness for entire length, in ventral view. Spatium intermetacarpale gradually becoming wider distally. Processus intermetacarpalis far proximally in spatium intermetacarpale.

REMARKS. Among extant Australo-Papuan Halcyonidae, *Tanysiptera* and *Melidora* have a low, flat processus dentiformis, *Syma* has an almost non-existent processus dentiformis as a barely raised roughened area, and *Todiramphus* and *Dacelo*, as well as Afro-Asian *Halcyon*, lack it (Boles unpubl. data). X-ray photography of study skins showed *Actenoides* and *Lacedo* have a low processus dentiformis, but *Halcyon* (*Pelargopsis*) and *Clytoceyx* do not. The x-rays, while sufficient for determining this process, are not adequate for detailed comparisons of these taxa. Other than size, there are not substantive differences between the carpometacarpi of *Todiramphus*, *Dacelo* (and presumably *Clytoceyx*); *Syma* differs only in its low processus dentiformis. Because *Dacelo* and *Clytoceyx* are considerably larger (*D. novaeguineae* 32.5–35.6mm), they are not considered further. Subse-

quent comparisons involve *Todiramphus*, *Syma*, *Tanysiptera* and *Melidora*.

The fossil (length 15.8mm) is in the size range of *Tanysiptera* (*sylvia* 14.0–15.2mm; *galatea* 15.2–16.5mm) and *Todiramphus* (*sanctus* 14.8–15.1mm; *macleayii* 14.5–15.7mm; *pyrrhopygia* 15.7–16.5mm; *chloris* 16.5–17.8mm). It is larger than *Syma* (*torotoro* 13.5mm; *megarhyncha* 14.4mm) and smaller than *Melidora macrorrhina* (18.9 mm). It differs from *Tanysiptera* and *Melidora* and resembles *Syma* and *Todiramphus* by being more slender and by having spatium intermetacarpale longer relative to the length of carpometacarpus and the dorsal rim of trochlea carpalis extending less distally relative to the ventral rim. The fossil differs from *Todiramphus* and resembles *Tanysiptera*, *Melidora* and *Syma* by having processus dentiformis present. This process, however, is narrow and pointed, rather than broad and flat as in these genera (and larger than in *Syma*), and is situated more proximally relative to the spatium intermetacarpale and processus intermetacarpalis than in *Tanysiptera* and *Melidora*, and more distally than in *Syma*. From all 4 genera, the Riversleigh specimen differs by having the caudal edge of os metacarpale majus straighter and less caudally concave, making os metacarpale majus thicker and spatium intermetacarpale proportionally narrower relative to the width of the carpometacarpus.

The significance of these differences is uncertain. They are individually minor, yet within the Halcyonidae the amount of variation in this bone is little so that these differences may assume greater importance. Variation in the carpometacarpus, however, is not representative of that of the remainder of the skeleton or indeed the rest of the morphology (Boles unpubl. data).

The fossil cannot be assigned to *Tanysiptera*, *Melidora*, *Syma* or *Todiramphus* and can be differentiated from extant species of these genera.

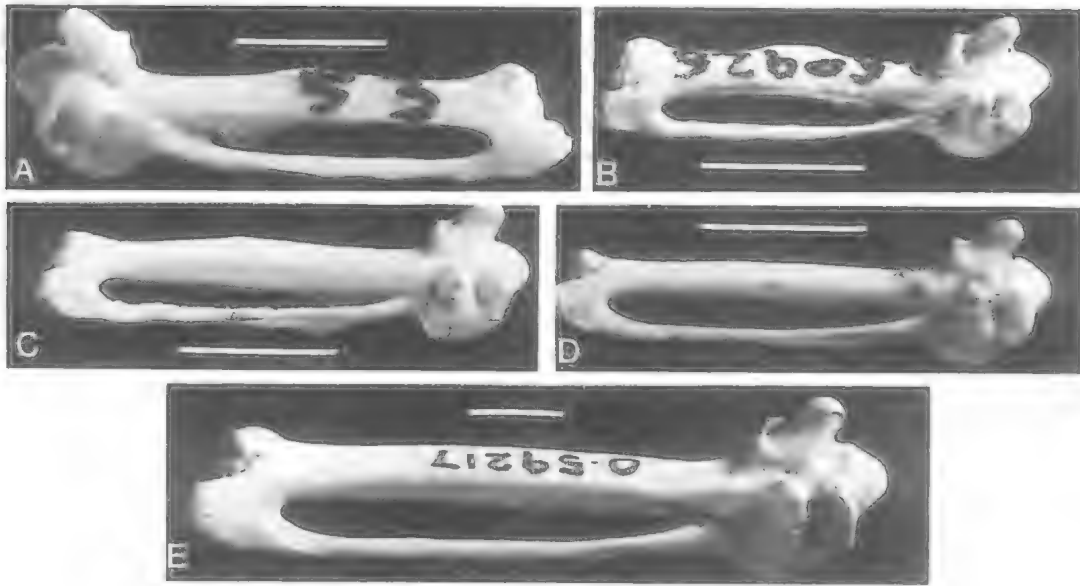


FIG. 1. Carpometacarpi of Australo-Papuan halcyonid kingfishers, in ventral view. All right side except for B. A, *Melidora macrorrhina* (ANWC CORS-53). B, *Tanysiptera sylvia* (AMO.60926). C, Riversleigh Halcyonidae gen. indet. (QMF29719). D, *Todiramphus sanctus* (AMO.57182). E, *Dacelo novaeguineae* (AM O.59217). Scales = 5mm.

Overall it has the greatest resemblance to species of *Todiramphus* in size and morphology, despite the presence of a small processus dentiformis. Given the relatively limited importance of carpometacarpal variation in the halcyonids and the limited fossil material it is imprudent to recognise a new genus at this time.

DISCUSSION

To place the Riversleigh fossil in perspective within halcyonid kingfisher evolution, the primitive members of the family must be identified. Fry (1980a, b) employed 3 criteria for this. Primitive kingfishers have 1) generalised diets and relatively unspecialised modes of foraging (i.e.: sitting and pouncing, non-fishing); 2, stable habitats and not of recent origin (rainforest), within which they may be discontinuously or relictually distributed; and 3, oligotypic genera (i.e. with few species) without close relatives. Fry (1980a) concluded that kingfishers (all families as recognised here) arose in Malesia, the area between Indo-China and the Coral Sea.

Prominent among the primitive forms were halcyonid kingfishers, many of which live in Malesian rainforests. Fry (1980a) speculated that 'the Daceloninae [= Halcyonidae] have a history of evolution in eastern equatorial rainforests al-

most as ancient as the mid-Cenozoic origin of the Alcediniformes [sensu Feduccia (1977)]'. By the early Miocene, the present geographical configuration of Malesia had been reached. This, in Fry's opinion, provided 'ideal circumstances for the multiplication of species, resulting in a fauna of forest-dwelling, non-fishing kingfishers ... At some more recent time, perhaps about the mid-Pliocene, this fauna gave rise to a lineage, *Halcyon* [s.l.], adapting to more open habitats'.

Under this suggested sequence of events, the rainforest-dwelling *Tanysiptera*, *Melidora*, *Actenoides* and *Lacedo* would be among the more primitive genera. *Todiramphus*, included by Fry (1980a) in his open habitat *Halcyon*, would be more derived. Presumably *Syma* (also included in *Halcyon* sensu Fry [1980a]) also was considered by Fry (1980a) to be a more derived taxon. Although entering open country adjacent to forest, the two species of *Syma* are essentially rainforest inhabitants, particularly in New Guinea (Coates, 1985).

In addition to sharing the primitive characters proposed by Fry (1980a, b), species of *Tanysiptera* and *Melidora* (as well as *Actenoides* and *Lacedo*) have a low but well-defined processus dentiformis on the carpometacarpus. This is absent in the other halcyonid genera examined, the Alcedinidae and Cerylidae, and some other cora-

ciiform families (e.g. Momotidae, Coraciidae). If any of these families is used for outgroup comparisons, the suggested polarity of the processus dentiformis is that its presence is derived. A similar comparison using other coraciiform families (Todidae, Phoeniculidae, Upupidae, Bucerotidae), in which the structure is present, gives the opposite conclusion: presence of the processus dentiformis is primitive, its absence derived. Within the Meropidae, the structure is present in some species (*Merops ornatus*) and absent in others (*M. apiaster*). The significance of this variation is unknown, as are the functional aspects of the processus dentiformis. Thus the polarity of this character's presence is not known. (This, of course, assumes that the processus dentiformis is homologous across the order. Whether this is so, and what relationship it has to the similar process found in the majority of the Passeriformes, is unknown.) Within the halcyonid kingfishers the presence of the processus dentiformis exhibits a strong correlation with Fry's (1980a,b) primitive criteria.

Superficially there seems to be little in common externally between *Melidora* and *Tanysiptera* beyond the basic kingfisher similarities. Each has specialised generic characters: a hooked bill in *Melidora* (Hooked-billed Kingfisher) and elongated, spatulate central rectrices in *Tanysiptera* (paradise kingfishers). *Melidora macrorrhina* is a rather drably coloured species. Other than blue scalloping on the crown, the plumage is a combination of browns and white. The underside is white, while the back, rump, tail, and wings are dark brown with paler brown scalloping. This plumage is quite unlike that of the paradise-kingfishers *Tanysiptera*, adults of which are strikingly patterned in unmarked blues and blacks, and usually either white or buff/rose. The juvenile plumage of *Tanysiptera*, however, is brown with scalloping, and Fry (1980b) was 'impressed by its [*Melidora*'s] plumage resemblance to the distinctive juvenile of *Tanysiptera galatea*'. That these two genera might be closely related was suggested by Fry (1980b), who thought it 'possible that *Melidora* and *Tanysiptera* are of immediate common descent and the former is a specialised derivative that has retained, in the adult, the ancestral juvenile plumage'. The presence of similar plumages is also evident in female *Lacedo* and some species of *Actenoides*, notably *A. princeps* and *A. lindsayi* of all ages. This resemblance between *Actenoides* and *Tanysiptera* and between *Lacedo* and *Melidora* was commented on by Fry (1980b).

Bell (1981) also considered that *Melidora* was closest to *Tanysiptera*. He noted that the call notes of these two species were similar and the distress notes identical. They have similar skeletal proportions, particularly in the relative length of the legs when compared to *Todiramphus*, *Halcyon* or *Dacelo* (Boles, unpubl. data). These two genera thus have more similarities than might be immediately obvious. They also share habitat preferences. Although *Melidora macrorrhina* and *Tanysiptera* species will enter mangroves, teak plantations and drier adjacent country, they are primarily occupants of rainforests. *Lacedo pulchella* and the 6 species of *Actenoides* inhabit rainforest, preferably in a primary, undisturbed state.

Species of *Todiramphus* are uniform in plumage. Most have a variation of the basic pattern of green or blue upperparts and white or light orange underparts and collar. Several subgroups can be discerned, but they still show only small divergences from this general form. These species are almost all sit and pounce feeders. Habitat preferences among species are more varied, ranging from rainforest to open country. Within Australo-Papua, however, few occur in rainforest and there is a decided bias towards open forest, woodland, mangroves, clearings and open country. Most rainforest inhabiting forms are found on islands of the southwest Pacific.

The processus dentiformis in the Riversleigh kingfisher is smaller than that in primitive modern forms. This could indicate that it has been undergoing reduction since the split of its lineage from that of *Tanysiptera-Melidora*. In this respect it is consistent with what would be predicted for a primitive species of *Todiramphus*. The bone exhibits a largely *Todiramphus* character while retaining this more primitive halcyonid feature.

The identification of the Riversleigh fossil as a halcyonid is compatible with Fry's (1980a) interpretation, as is considering the presence of the processus dentiformis as primitive. According to Fry's scenario, an early Miocene kingfisher should be a primitive form. His criteria, however, are not useful in this situation. The foraging methods of the fossil cannot be determined, nor can its systematic isolation be ascertained. The Riversleigh habitat is considered (Archer et al., 1992) to have been rainforest, but this cannot be used as a character for making a taxonomic determination.

Although this fossil permits identification as a halcyonid kingfisher, it is not clear whether this species belongs to an existing genus or should be

allocated to a new one. The presence of a feature found in living primitive genera and the kingfisher's occurrence in what is considered to have been rainforest suggest that it, too, was a more primitive form. This is consistent with the sequence of evolutionary events suggested by Fry (1980a).

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HINDLIMB PROPORTIONS AND LOCOMOTION OF *EMUARIUS GIDJU* (PATTERSON & RICH, 1987) (AVES: CASUARIIDAE)

WALTER E. BOLES

Boles, W.E. 1997 06 30: Hindlimb proportions and locomotion of *Emuarius gidju* (Patterson & Rich, 1987) (Aves: Casuariidae). *Memoirs of the Queensland Museum* 41(2): 235-240. Brisbane. ISSN 0079-8835.

Using proximal and distal fragments, the length of the tarsometatarsus of *Emuarius gidju* is estimated and compared to that of other hindlimb elements. From these proportions and other hindlimb morphology, the inferred locomotory mode of *E. gidju* is compared with Recent casuariids. *Emuarius gidju* appears to have been more cursorially adapted than *Casuarius* and dwarf *Dromaius*, suggesting at least some open habitat in the Riversleigh palaeoenvironment. Using the relationship between weight and least circumference of the femur and tibiotarsus in Recent birds, the weight of *E. gidju* is suggested to have been 19-21kg. □
Emuarius, Aves, hindlimb, locomotion.

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Emus, *Dromaius* (Dromaiinae), form a prominent element of Australia's avifauna. The closely related cassowaries, *Casuarius* (Casuariinae), are more restricted in distribution. These two groups occupy very different modern habitats, and locomotory adaptations correlated with these different habitats are obvious in the relative proportions of the lower limb bones. Because of the relationship between habitat and limb proportions, fossil emus and cassowaries are potentially good palaeoenvironmental indicators. Emus have a better fossil record (Patterson & Rich, 1987), than cassowaries (Vickers-Rich, 1991). Patterson & Rich (1987) described lower limb elements from the Miocene of central Australia as a small emu, *Dromaius gidju*. Boles (1991) erected *Emuarius* for this species and considered it closer to emus than cassowaries, but nearer their dichotomy than any other described taxon.

The type material of *Emuarius gidju* is part of the Kutjamarpu Local Fauna, recovered from the Leaf Locality (UCMP V-6213) on the E shore of Lake Ngapakaldi in the E Lake Eyre Sub-Basin, South Australia. Much *E. gidju* material occurs at Riversleigh NW Queensland. Archer et al. (1989, 1994) considered the Riversleigh palaeohabitat as rainforest, based on mammal remains.

This paper is to 1) estimate the lower limb proportions of *E. gidju*; 2) compare these to modern emus and cassowaries and, by implication, to their style of locomotion; 3) make an initial estimate of the weight of *E. gidju*; and 4) interpret the possible palaeohabitat at Riversleigh where *E. gidju* occurs.

MATERIALS AND METHODS

Osteological terminology follows Baumel & Witmer (1993). Measurements were made with vernier calipers accurate to 0.05mm and rounded to the nearest 0.1mm. Institutional acronyms are AM (Australian Museum), QM (Queensland Museum) and SAM (South Australian Museum).

The type specimen of *E. gidju* (SAMP26779) is an associated distal tibiotarsal fragment, proximal tarsometatarsus including much most of the shaft, and complete set of pedal phalanges (Patterson & Rich, 1987) and numerous specimens of *Emuarius* are known from Riversleigh (Table 1).

To compare changes in relative proportions of the casuariid hindlimb, the following measures were calculated for the bone lengths of the 3 extant species of *Casuarius* and the 1 living and 2 recently extinct dwarf species of *Dromaius*:

$$TBT/FMR = \frac{\text{Tibiotarsus} \times 100}{\text{Femur}}$$

$$TMT/FMR = \frac{\text{Tarsometatarsus} \times 100}{\text{Femur}}$$

$$TBT/TMT = \frac{\text{Tibiotarsus} \times 100}{\text{Tarsometatarsus}}$$

Because the purpose was to find general, rather than detailed, directions of change, measurements were taken from the literature (Table 2) and rounded to the nearest mm. Means were used where available. The sample sizes were often small, sometimes comprising single individuals.

Predicted body weight of *Emuarius gidju* was calculated (Campbell & Marcus, 1991) from AM F78585 (near complete femur) and QMF16827

(distal tibiotarsal fragment). Tape was wrapped around the bones at their least circumferences, marked at the point of overlap, straightened and measured with calipers. These results were used in the equation $\log_{10}(\text{weight}) = a \cdot \log_{10}(\text{circumference}) + b$, where the values of a (slope) and b (intercept) were those determined by Campbell & Marcus (1991) for all birds for the respective elements (femur: $a=0.411$, $b=-0.065$; tibiotarsus: $a=2.424$, $b=0.076$).

RESULTS

Increased cursoriality in these birds is associated with an increase in the lengths of the tibiotarsus and tarsometatarsus relative to that of the femur (Howell, 1944). Relative proportions of the hindlimb contributions of the long bones in *Casuarus*, *Dromaius* and *Emuarius* (Fig. 2) show that that of the tibiotarsus remains more or less consistent in all taxa; that of the femur decreases with increased cursoriality, whereas that of the tarsometatarsus increases. The relationship between these changes is consistent for Recent species: $\text{TBT/FMR} = 0.45 [\text{TMT/FMR}] + 113$; $r=0.84$.

These changes appear independent of overall size when compared between genera, but within genera the smaller members have the greater TBT/TMT and smaller TMT/FMR. The TBT/FMR in *Casuarus* remains constant. It suggests from these figures that the smaller species in each genus are the least cursorial members.

The Kutjamarpu femur (AMF78585; Boles, 1991) of *E. gidju* is 194mm long, which, because of abrasion, is a few mm less than its original length, of about 198mm and very likely not 200mm. Complete tibiotarsi are unknown for *E. gidju* (Table 1). Nevertheless, it is possible to predict the size and relative proportions of this bone from other hind limb elements. Tarsometatarsi are represented by the holotypical proximal end and shaft, and several distal fragments. An estimate of the tarsometatarsal length was made by using the proximal end and shaft and a distal fragment. The proximal tarsometatarsal fragment is 276mm long; the longest edge of its shaft is straight and shows no evidence of flaring outward to trochlea metatarsi II. The distal piece is 64mm long; the small portion of shaft remaining is just proximal to the flaring of trochlea metatarsi II. Because there is little, if any, overlap between these two pieces, minimum length of the tarsometatarsus is 340mm (Fig. 3).

TABLE 1. Specimens that have been referred to *Emuarius gidju*. *=specimens described by Boles (1991).

SITE	REG. NO.	ELEMENT
Lake Ngapakaldi	SAM P26779	Holotype: associated distal tibiotarsus, proximal tarsometatarsus, complete pes
	AMF78585*	Femur
Riversleigh		
System A or B White Hunter	QMF16827*	Tibiotarsus
System B Camel Sputum	QMF29720	Vertebrae
	QMF29721	Vertebrae
	QMF16828*	Femur
	QMF16829*	Femur
	AMF78586*	Tibiotarsus
	QMF29722	Tibiotarsus
	QMF29723	Tarsometatarsus
	QMF29724	Tarsometatarsus
	QMF29725	Tarsometatarsus
	QMF29726	Tarsometatarsus
	QMF29727	Tarsometatarsus
Upper	QMF16830*	Rostrum
	QMF16831*	Scapulocoracoid
	QMF29728	Vertebrae
System ?B, Dirks Towers	QMF29729	Tarsometatarsus
System C Gag	QMF16832*	Femur
	AMF78587*	Tarsometatarsus

Using a tarsometatarsal length of 340mm and a femoral length of 198mm, gives a TMT/FMR of 172, greater than that of any Recent casuariid except *Dromaius novaehollandiae*. Using these values with the regression equation for the family (Fig. 4) gives a predicted TBT/FMR of 190, which corresponds to a tibiotarsal length of 376mm. These 3 values give a combined length of 916mm, virtually the same as the hindlimb of *Casuarus casuarus*, although the proportional contribution of each bone to this length is different (Fig. 2).

This figure must be used with caution. The fragments on which it is based represent different individuals from different localities. As such, there are several sources of potentially significant variation between components. Geographical variation may not have been of major importance; living *D. novaehollandiae* exhibits little differentiation across its range. There is much greater size variation across this species' chronological



FIG. 1. Leaf Locality femur of *Emuarius gidju* compared with femora of Recent casuariids, in cranial view. From left, *Casuarius Casuarius*, *C. bennettii*, *Emuarius gidju*, *Dromaius novaehollandiae* and *D. ater*.

range, with mainland fossils usually smaller than modern birds. Patterson & Rich (1987) suggested that it 'may have been at any one time in the Pleistocene both larger or smaller than at present'. Considerable intraspecific variation in living *D. novaehollandiae* is probably related to age and sex, as well as individual differences (Marchant & Higgins, 1990). For example, among 22 modern specimens, Patterson & Rich (1987) found a range in tarsometatarsal length of 332–422mm (mean 383mm; s.d. 18.0).

Miller (1963) described *Dromaius ocypus* from the middle to late Pliocene Palankarinna Local Fauna from Lake Palankarinna, northern South Australia. This species was intermediate in size between *Emuarius gidju* and living *Dromaius novaehollandiae*. The tarsometatarsus of *D. ocypus* is markedly shorter relative to its width than is that of *D. novaehollandiae*, but less so than in *Casuarius*. Vickers-Rich (1991) interpreted this as suggesting a less cursorial lifestyle for *D. ocypus* than for *D. novaehollandiae*. Because Patterson & Rich (1987) did not give comparative figures for relative widths, it is difficult to quantitatively compare *E. gidju* with these species. Visually, *Emuarius* appears to be proportionally thinner for its length than is *D. ocypus*, but not to the degree of *D. novaehollandiae*.

Patterson & Rich (1987) pointed out that, although, the foot of *E. gidju* is more like that of emus than cassowaries, it is more cassowary-like

than any known species of emu (illustrated in Patterson & Rich, 1987). In emus, phalanx ungualis of digit III is longer than that of digit II, whereas in cassowaries it is reversed, with phalanx ungualis of digit II extended into a long spike several times the length of phalanx ungualis of digit III. *Emuarius* does not have phalanx ungualis of digit II developed into a spike, but it is still longer than that of digit III.

Cassowaries have digits II and IV relatively long compared with digit III (ratios of II:III and IV:III, respectively, without phalanges ungualis 0.82, 0.76). Both are substantially reduced in relative length in emus (ratios as above – 0.55, 0.63). Both digits II and IV of *Emuarius* are comparatively

longer than those in emus (digit IV to a lesser degree), but not to the extent seen in cassowaries (0.57, 0.68). Patterson & Rich (1987) suggested that the reduction of digit IV and particularly of digit II in *E. gidju*, compared with the highly cursorial *D. novaehollandiae*, appears to parallel similar reductions in other groups of terrestrial birds and mammals.

In comparison with the pedal phalanges of cassowaries, those of emus are dorsoplantarly compressed. *Emuarius* is somewhat intermediate, with its phalanges substantially more dorsoplantarly compressed than those of cassowaries, but less compressed than (but more similar to) the condition in emus.

Campbell & Marcus (1991) stated 'the least shaft circumference of either [femur or tibiotarsus] can be a reliable indicator of the weight of a fossil bird'. From their equation, and measurements of *E. gidju* bones, predicted weights of this species were 21kg based on the femur and 19kg based on the tibiotarsus. The least circumference of the tibiotarsus is almost always at or distal to the midpoint of the bone; in most birds it is in the distal third (Campbell & Marcus 1991). No tibiotarsal specimen of *E. gidju* is complete, although the length of that measured is about a third of the predicted length for this bone. It is possible that the least circumference occurs on the missing section of tibiotarsus, and the value given here would have to be adjusted. The predicted

TABLE 2. Measurements (mm) and measures of relative proportions of hindlimb bones of Recent emus and cassowaries and of *Emuarius gidju*. For calculation of predicted measurements of *E. gidju* and of measures of relative proportions, see text.

Species	FMR	TBT	TMT	Source	TBT/ FMR	TMT/ FMR	TBT/ TMT
<i>Dromaius novaehollandiae</i>	203	401	383	Patterson & Rich, 1987	198	189	105
<i>Dromaius baudinianus</i>	164	293	234	Morgan & Sutton, 1928	179	143	125
<i>Dromaius ater</i>	178	331	274	Morgan & Sutton, 1928	186	154	121
<i>Casuaris unappendiculatus</i>	236	388	306	Rich et al., 1988	164	130	127
<i>Casuaris casuaris</i>	232	384	300	Rich et al., 1988	166	129	128
<i>Casuaris bennetti</i>	221	365	229	Rich et al., 1988	165	104	159
<i>Emuarius gidju</i>	198	376	340	This paper	190	172	111

weights from the two bones are close enough to give an acceptable first estimate for *E. gidju*.

DISCUSSION

Throughout the early Tertiary, much of Australia was covered in closed forest, and the climate was considerably more humid than at present (Frakes et al., 1987). The dominant vegetation type over much of the continent was rainforest. *Nothofagus*-dominated rainforest covered the Lachlan River valley during the late Eocene to late Oligocene-early Miocene (Martin, 1987). Even where closed forests were not present, gallery rainforest probably occurred along

watercourses. It was not until at least the middle Miocene (c. 15 mya) that drying of the climate began and open habitats started to appear on a large scale. There is no evidence of grasslands before the end of the late Miocene to Pliocene (Martin, this volume).

The graviportal locomotion of *Casuaris* is associated with movement through the dense vegetation of the Australo-Papuan rainforests. Increased cursoriality seems correlated with the appearance of more open habitat, in which sustained running could take place. (While able to run if required, cassowaries have

limited opportunities in such habitat to work up and sustain a reasonable degree of speed because sufficiently open areas are restricted.) Morphological correlates with cursoriality include proportional lengthening of the tibiotarsus and tarsometatarsus, and a reduction in the relative size of digit II. Conditions between the extremes of the states found in *Casuaris* and *Dromaius* are suggestive of levels of cursorial ability intermediate between theirs, although at what point along the scale cannot be determined. This, in turn, suggests the possibility that the amount of open habitat might be also somewhere between that available to cassowaries and emus.

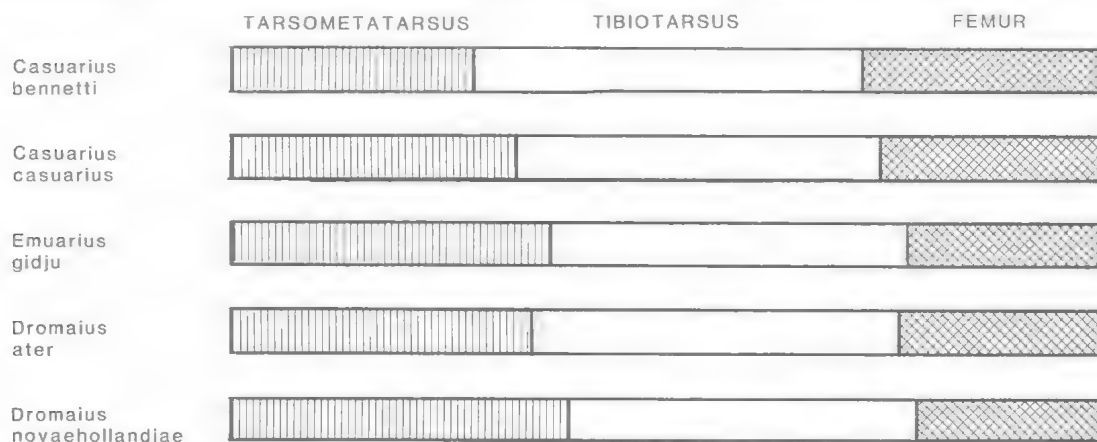


FIG. 2. Comparative proportions of bones in the hindlimbs of *Emuarius gidju*, two species of *Casuaris* and two species of *Dromaius*. Note that while the tibiotarsal proportion remains relatively constant, the proportion comprising the femur decreases as that of the tarsometatarsus increases.

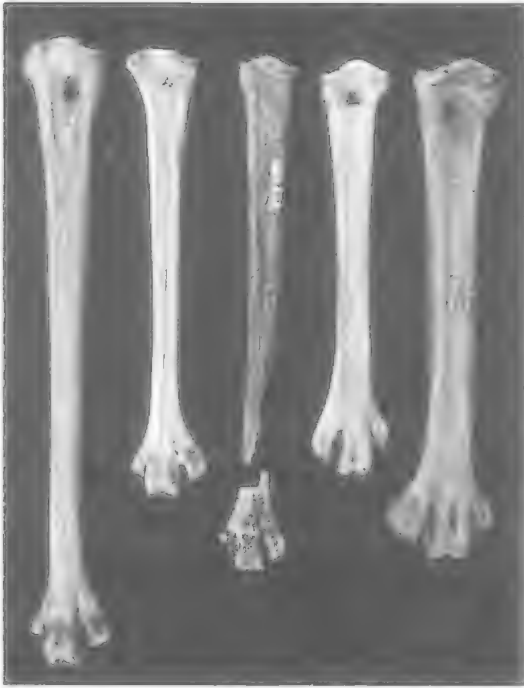


FIG. 3. 'Combined' length of Leaf Locality proximal tarsometatarsus and Riversleigh distal tarsometatarsus compared with tarsometatarsi of Recent casuariids, in cranial view. From left, *Dromaius novaehollandiae*, *D. ater*, *Emuarius gidju*, *Casuarius casuarius* and *C. bennettii*.

Casuarius has been considered more primitive than *Dromaius* on the basis of distribution, habitat preferences and hindlimb. Schodde & Calaby (1972) and Schodde (1982) cited the cassowaries as elements of the Tumbunan avifauna, which represents the earliest lineages of extant Australo-Papuan birds. The emus were placed by Schodde (1982) in the autochthonous Eyrean fauna, which evolved in response to the opening of the Australian habitat. Boles (1991) considered *Emuarius* to be closer to the dichotomy of cassowaries and emus than any other known taxon, but too cursorially adapted and *Dromaius*-like to have been the common ancestor. It appears to mark in the Casuariidae a stage in the transition from a graviportal to a more cursorial locomotion. Although some characters of the hindlimb of *E. gidju* are more similar to either *Casuarius* or *Dromaius*, many are intermediate between living members of these genera (Boles, 1991). Boles (1991) drew attention to the fact that the lower limb bones were more similar to those of *Dromaius*, whereas the femur, whose proportions are more dependent on the bird's mass than its

locomotion (Prange et al., 1979), more closely resembled *Casuarius*.

There are alternative explanations that accommodate both the cursorial hindlimb proportions of *E. gidju* and the absence of open spaces. One possibility is that the ground cover of the rain forests was sufficiently open for cursorial animals to move rapidly without obstruction. For example, modern *Nothofagus* forests are frequently open below the canopy, without the dense understory of some other rain forest types (pers. obs.).

Neville Pledge (pers. comm.) suggested that a situation may have existed similar to that which occurred on Kangaroo Island when the dwarf emu *Dromaius baudinianus* was extant. Much of the island's vegetation was very thick and would have prevented rapid passage of a large animal such as the emu. Large mammals, however, forced runways through the vegetation, permitting them to move with comparable, albeit restricted, ease. The emus apparently took advantage of these runways for their own progress. Likewise, the large mammals known from Riversleigh may have opened similar pathways through the thick undergrowth, which could have been used by *E. gidju*. Nonetheless, *D. baudinianus* was also noted for being very fast and virtually uncapturable in open areas.

A small Miocene dromaiid from Alcoota, NT, is known from 2 phalanges and 3 unassociated trochleae (Patterson & Rich, 1987). These are of comparable size with *E. gidju*. There are slight differences in phalangeal morphology, and Patterson & Rich (1987) retained these specimens as *Dromaius* sp. indet. until more complete material is available. The Alcoota palaeohabitat has been interpreted as a lake, bordered by sedge or grassland, grading to woodland and gully forest (Murray & Megirian, 1992). This is a different environment than that interpreted for the older Riversleigh deposits. Even if the Alcoota dromaiid proves to be *E. gidju*, it would have limited relevance to reconstructing the Riversleigh habitats because of the age differences of the deposits. It would, however, suggest that *E. gidju* was preadapted for the more open Alcoota environment.

Models of this species' locomotory mode depend on extrapolations from living, non-congeneric relatives. These are speculative, and must be treated as such, while palaeoenvironmental reconstructions based on them require an even greater degree of caution.

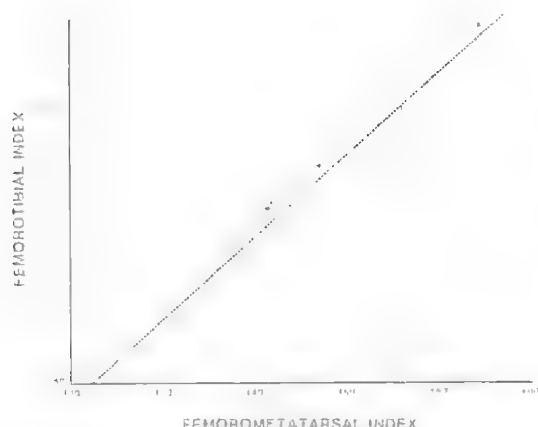


FIG. 4. Relationship of TMT/FMR and TBT/FMR of Recent species of *Casuarius* (open circles) and *Dromaius* (closed circles). Species numbered as follows: 1. *Casuarius bennetti*; 2. *C. casuarius*; 3. *C. unappendiculatus*; 4. *D. baudinianus*; 5. *D. ater*; 6. *D. novae-hollandiae*. Regression line is $TBT/FMR = 0.45 [TMT/FMR] + 1.13$; $r = 0.84$. The line vertical line represents the intersection with this line of the TMT/FMR (1.72) for *Emuarius gidju* as calculated in the text. Predicted TBT/FMR is 1.90.

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RIVERSLEIGH BIRDS AS PALAEOENVIRONMENTAL INDICATORS

WALTER E. BOLES

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Fossilised birds from Riversleigh are used to make a palaeoenvironmental reconstruction. Difficulties that hamper this attempt are discussed. From the early to early late Miocene deposits, a range of taxa demonstrate aquatic situations; four others are indicative or at least suggestive of rainforest; one hints at at least some open spaces; and six are ambiguous because of insufficient morphological variation between taxa with different ecological preferences or insufficiently known palaeobiology. The only species thus far identified from Pliocene Rackham's Roost Site points to conditions similar to those at Riversleigh today. □
Riversleigh, birds, palaeoecology.

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Modern birds are excellent habitat indicators. Potentially, the Tertiary avifauna of Riversleigh could serve a valuable role in interpreting the palaeoenvironment. Numerous bird remains have been recovered, but few have been studied (Rich, 1979; Boles, 1991, 1993a, b, c, 1995, 1997a, b).

Based primarily on the diverse mammal remains, Archer et al. (1989) interpreted the vegetation of Riversleigh during the early to early late Miocene as 'dense, species-rich gallery rainforests probably similar to those that persist today in mid montane New Guinea'. Archer et al. (1994) concluded that the surrounding Pliocene habitat was 'a dry sclerophyll forest or woodland with a grassy understorey, probably not too unlike the environment that dominates Riversleigh today'. This paper reviews available information about Riversleigh birds as it might contribute to interpretations of Tertiary environments.

Material (Table 1) is lodged in the Queensland Museum (QM) and Australian Museum (AM). The geology and geography of the Riversleigh deposits are available elsewhere (Archer et al., 1989, 1994, 1995; Megirian, 1992).

INTERPRETATION OF HABITATS: BASIC TENETS

One of the most striking features of the Riversleigh avifauna is the large proportion of small terrestrial forms compared to other middle Tertiary sites in Australia, which are largely dominated by waterbirds and larger, flightless forms, both of which are also present at Riversleigh. Among modern Australian terrestrial (non-aquatic) birds, the prevailing pattern is considered to be that the more primitive (least

specialised) members of lineages are found in montane and subtropical rainforest and contiguous wet forests, whereas the more derived taxa occur in open habitats. Schodde & Faith (1991) considered that 'rainforest-inhabiting members, particularly in montane New Guinea and subtropical Australia, represent ancestral forms from which those in scleromorphic vegetation have been derived'. These ancestral components have been recognised as the Tumbunan fauna (Schodde & Calaby, 1972; Schodde, 1982; Schodde & Faith, 1991). The Tumbunan avifauna is now largely centred on 'a *Nothofagus*-myrtle-podocarp-dominated forest of the type once widespread across Australia through the mid Tertiary' (Schodde, 1982), although some elements of this fauna now extend well beyond this habitat. Although the Tumbunan-type habitat is now mostly restricted to higher elevations, a distribution that is relictual, it was once more widespread through lower altitudes. Schodde & Faith (1991) suggested that 'the subtropical Tumbunan avifaunas now present in montane New Guinea were widespread in Australia' in the mid-Tertiary. Thus the habitat of Riversleigh during the Miocene was probably similar to that retained in these present Tumbunan refuges.

This apparent relationship between level of specialisation and habitat has been adopted as a basis for palaeoenvironmental interpretation. A fossil taxon is tentatively considered a likely rainforest inhabitant if it is primitive in its lineage. It may also be considered to occur in rainforest if its affinities are to a group that is today confined to rainforest. If all living species occur in a certain habitat then that habitat is considered to most likely for the fossil form.

mated hindlimb proportions of *E. gidju* with those of Recent *Dromaius* and *Casuaris*. The tibiotarsus and tarsometatarsus of *E. gidju* were rela-

lower leg permits these birds to capture prey from hollows and recesses inaccessible to other predatory birds. Modern species occur in a range of

There seems little problem with freshwater aquatic birds. Within a family, there may be some variation in the type of aquatic habitats preferred, although the range of differences is substantial in only a few instances. Modern habitat preferences are used as an indication of the fossils' palaeohabitats, unless otherwise indicated.

Unless there is some outstanding morphological feature that signals a major shift in its biology, a fossil bird is considered to have similar ecological characteristics as its modern counterparts. Similarities in morphology between fossil and living forms are interpreted to share similar functions, unless there is evidence to the contrary.

SYSTEMATIC LIST

Dromornithidae

This extinct family comprises 8 species in 5 genera (Rich, 1979). These were large, flightless birds with major, 'ratite'-grade modifications to an entirely terrestrial lifestyle. The extent of these masks any relationships to other known orders of birds, although this family is no longer considered closely allied to living ratites (Olson, 1985).

Barawertornis tedfordi and *Bullockornis planei* occur at Riversleigh as conspicuous faunal elements at some sites because of their abundance and size. Despite this, they are limited palaeoenvironment indicators because little is understood of their biology. The 2 monotypic Riversleigh genera are among the least known.

At Riversleigh, the 2 species occur together, often, but not always, with other large animals (e.g., D-Site). At several sites they occur with aquatic animals such as lungfish, turtles and crocodiles. Whether this is an indication of a water-side association or a taphonomic artefact is not known. Nothing in the foot structure is obviously modified for entering water, nor has there been previous suggestion of an aquatic association.

Relative proportions of the hindlimb bones can be a useful indication of locomotory mode. In few dromornithid species, however, are complete specimens known for all major leg elements, and these rarely represent the same individual. Reconstructions must necessarily be based on the better known forms, particularly *Genyornis newtoni*. Estimates of leg proportions are based on measurements given by Rich (1979). The hindlimb proportions of most dromornithids are very different from those of *Casuarius* or *Dromaius*, with only *Ilbandornis lawsoni* having proportions approaching those of living emus; Rich (1980) and Vickers-Rich (1991) considered

this the most cursorial species. Where known, the tarsometatarsus of other species is short relative to the other long bones, more like the moas.

The moas (Worthy, 1991) provide some suggestions about aspects of dromornithids' lifestyle. Most moas were forest dwellers, almost exclusively herbivorous. None seemed adapted to cursorial locomotion. Moa remains are often recovered in large numbers, indicating that these were gregarious birds. Many Australian dromornithid sites yield large numbers of specimens, indicating aggregations. Such a concentration of animal biomass is analogous to moas and suggests that dromornithids were herbivorous (Vickers-Rich, 1991).

The dromornithid bill was much heavier and deeper than the moas' (Olson, 1985, fig. 3; Vickers-Rich, 1991, pl. 4). The skull was larger and more robust, with scars indicating broad attachments for the jaw muscles (P. Vickers-Rich pers. comm.). Regardless of what dromornithids ate, they were equipped to handle more substantial food items than were moas. Their bills are not hooked or otherwise suggestive of a predator.

Unlike moas, no remains of dromornithid food have been found. Large accumulations of dromornithid gastroliths (gizzard stones) occur at Riversleigh (Archer et al., 1994:79) and other sites (Stirling & Zeitz, 1900; Vickers-Rich, 1991).

By the late Miocene, both graviportal and cursorial species lived in northern Australia. This was taken to indicate both forest and open country by Rich & Baird (1986), who did not consider dromornithids to have been particularly successful in invading grasslands. The Riversleigh fossil material does not show cursorial modifications. It can be tentatively concluded that *Barawertornis* and *Bullockornis* were forest dwellers.

Casuariidae - emus and cassowaries

Emuarius Boles, 1991 occurs at Riversleigh. Living emus and cassowaries *Casuarius* are quite different in their habitat preferences and locomotory styles. The latter is reflected in the hindlimb, suggesting potential for inferring palaeohabitat from a comparison of *E. gidju* with living forms.

Patterson & Rich (1989) found that the phalanges of *E. gidju* were between those of *Dromaius novaehollandiae* and *Casuarius* in morphology, although more similar to the former in relative lengths and in degree of dorsoplanar compression. The fossil form *D. ocybus* Miller, 1963 had a tarsometatarsus that is markedly shorter relative to its width than that of *D. novaehollandiae*, but longer than *Casuarius*. Vickers-Rich (1991) in-

TABLE 1. Bird families in Riversleigh Tertiary deposits and sites from which these have been recovered. A=Dromornithidae; B=Casuariidae; C=Phalacrocoracidae; D=Ciconiidae; E=Anatidae; F=Accipitridae; G=Rallidae; H=Cacatuidae; I=Psittacidae; J=Apodidae; K=Halcyonidae; L= Passeriformes (¹=Menuridae; ²=Oriolidae; ³=Orthonychidae).

SITE	A	B	C	D	E	F	G	H	I	J	K	L
SYSTEM A												
D-Site	X											
D-SITE EQUIVALENT												
Sticky Beak	X					X						
SYSTEM A OR B												
White Hunter		X		X	X	X	X					X
SYSTEM B												
Camel Sputum	X	X	X				X			X		X
Helicopter	X											
Outasite										X		X
Panorama												X
RSO	X							X		X		X
Upper	X	X										X ¹
Wayne's Wok	X		X									X
Wayne's Wok II												X
Neville's Garden	X											X ²
SYSTEM ?B												
Bitesantennary				X								
Dirks Towers		X										X
Microsite												X
SYSTEM C												
Archie's Absence												X
Henk's Hollow												X
Gag		X										X
Gotham												X
Jim's Carousel												X
Last Minute											X	X ³
Ringtail						X		X				X
Two Trees												X
PLIOCENE												
Rackham's Roost									X			X

terpreted this to mean that *D. ocypus* was less cursorial than *D. novaehollandiae*. *Emuarius gidju* approaches *D. novaehollandiae* in tarsometatarsal length:width ratio more closely than does *D. ocypus* (Boles, this volume a).

Increased cursoriality in the Casuariidae is characterised by an increase in the lengths of the tibiotarsus and tarsometatarsus relative to the femur. Boles (this volume a) compared the estimated hindlimb proportions of *E. gidju* with those of Recent *Dromaius* and *Casuarius*. The tibiotarsus and tarsometatarsus of *E. gidju* were rela-

tively longer than in any other casuariid, except *D. novaehollandiae*. The structure of the phalanges, relative width of the tarsometatarsus and proportions of the hindlimb suggest that *E. gidju* was more cursorial than *Casuarius* and may have approached the ability exhibited by *D. novaehollandiae*. *E. gidju* may have had habitat preferences resembling those of *D. novaehollandiae*, i.e., largely open country, although some rainforest types could possibly offer a sufficiently open understorey.

Phalacrocoracidae - cormorants

A distal carpometacarpal fragment comes from a large cormorant. Beyond signaling a lacustrine situation, it is uninformative.

Ciconiidae - storks

Stork remains comprise 1 proximal and 2 distal tarsometatarsal fragments, 1 quadrate and a partial skull. The tarsometarsi do not belong to *Ephippiorhynchus*, the only living genus in Australia, and are probably referable to *Ciconia*, a genus now found in Eurasia, South America and Africa. All living storks have associations with shallow, slow moving water, although they are not restricted to aquatic habitats; they do not enter heavily forested areas. All eat small animals, including vertebrates, and some (*Leptoptilos*) consume carrion.

Anatidae - waterfowl

Several specimens have been allocated to this family but no further determination has been made. Subgroups of living waterfowl have circumscribed habitat preferences. The Riversleigh specimens indicate aquatic, probably lacustrine, situations.

Accipitridae - diurnal birds of prey

Pengana robertbolesi, a large bird of prey, with hyperflexible tarsal joint (Boles, 1993a) is convergent with the living *Polyboroides* (Africa) and *Geranospiza* (South America). Mobility of the lower leg permits these birds to capture prey from hollows and recesses inaccessible to other predatory birds. Modern species occur in a range of

habitats and do not permit any meaningful extrapolation to Riversleigh. A femoral fragment of this family is of comparable size to *Pengana*, but can be referred only tentatively to this taxon.

Rallidae - rails

There is much rail material, representing most forelimb and hindlimb elements, from several sites, but most abundantly at White Hunter site, possibly from a single individual. All specimens represent a medium-sized rail about the size of living *Gallinula tenebrosa*. From the shape of the carpometacarpus and the relative sizes of the wing and leg elements, it appears to have been flightless. This rail is probably related to the native-hens *Tribonyx*, now usually merged as a subgenus of *Gallinula*. The native-hens comprise two living endemic Australian species, one of which is flightless, and a flightless Pleistocene species endemic to New Zealand. Although largely remaining in the vicinity of water, both Australian species freely enter adjacent open country. The flightless Tasmanian *mortierii* enters cultivated paddocks, and mainland *ventralis* may move some distance from water in semiarid and arid regions. Species of *Gallinula* are gregarious, which is consistent with the number of fossils found at some sites. The Riversleigh rail indicates the proximity of wetlands, but little else about the local environment.

Cacatuidae - cockatoos

A rostrum has been referred to the modern white cockatoos, *Cacatua* (Boles, 1993b). Within Australia, these species occur from rainforest fringes through open forest and woodland to open arid country. The Riversleigh bird is considered to have been similar to the group of white cockatoos with small bills and rounded, uncoloured crests, such as the corellas. These species exhibit a considerable range of habitat preferences, from central Australian arid zone (*C. pastinator*) to rainforests on some islands e.g., Solomon Islands (*C. ducorsii*). This range of habitats occupied by modern species renders the Riversleigh specimen of little value in palaeohabitat reconstruction.

Psittacidae - parrots

Two carpometacarpi and a tarsometatarsus from Rackham's Roost come from the living Budgerigar *Melopsittacus undulatus*. This is a good indication that the Pliocene habitat at Riversleigh was open and lightly timbered. Today this species occurs in the arid, semi-arid

and subhumid zones, including Riversleigh, but never far from water.

Apodidae - swifts

Humeri, a coracoid and tarsometatarsus of a medium-sized swift are close to a large species of swiftlet *Collocalia*, the only genus that breeds in Australia at present. These species nest in caves, but, despite the number of apparent Riversleigh deposits originating from cave floors, surprisingly few remains have been found at Riversleigh thus far. One of the bones is that of a young bird, strong indication that at least some level of local breeding was taking place. Swifts are not good environmental indicators, because they are aerial feeders, capturing flying insects above the habitat canopy, irrespective of what that habitat may be.

Halcyonidae - forest kingfishers

The single specimen available is assigned to the Halcyonidae, possibly close to *Todiramphus* (Boles, 1997b) and similar to more primitive living halcyonids (*Tanysiptera*, *Melidora*, *Syma*), which are rainforest inhabitants (Fry, 1980a,b). The Riversleigh fossil resembles what would be predicted for an early member of the *Todiramphus* lineage. Australian *Todiramphus* occur outside rainforest, but species of the genus live in rainforests in other parts of Australasia.

Passeriformes - songbirds

These birds are good habitat indicators at specific or generic level. Songbirds are known from about 100 specimens from at least 20 sites (Boles, 1995); however, only 3 specimens thus far provide useful habitat indications. *Orthonyx kaldwinnyi*, of which a femur has been reported (Boles, 1993c), belongs to a genus with the 2 living species confined to rainforest of the east coast and New Guinea, occasionally entering dense bordering vegetation (e.g., *Lantana*). Green Waterhole Cave, SE South Australia, the site for *O. hypsilophus*, never had rainforest, but there is evidence for a thick cover of *Leptospermum* (Baird, 1985), which would probably have provided adequate cover.

The lyrebird *Menura newmanoides* is represented by a carpometacarpus (Boles, 1995). The two living species occupy rainforest and, in the case of *M. novaehollandiae*, contiguous forest. The habitat preferences of the Riversleigh species of *Orthonyx* and *Menura* are assumed to be similar to those of their modern congeners.

A large lower mandible from Neville's Garden Site (unpubl. data) is from the Oriolidae which

includes the frugivorous forest birds *Oriolus* and *Sphecotheres viridis*; many occur in closed forest. The fossil suggests rainforest, but is not diagnostic.

TAPHONOMY

None of the aquatic or semi-aquatic species, except the *Gallinula*-type rail, show any evidence of unusual causes of death or accumulating agents. The rails occur in greater numbers at a handful of sites, possibly due to a gregarious habit rather than taphonomy. Dromornithid remains being very common at some sites may also be a result of gregariousness or their corpses could have been accumulated during flooding. They are often found with large aquatic taxa (e.g., lungfish, turtles, crocodiles), and these may represent thanatocoenoses. Most other terrestrial species are too infrequent to provide any clues, but may be best considered chance survival of the remains of animals that died for a variety of reasons.

Exceptions are the small terrestrial forms, particularly passerines, which appear to have been killed by ghost bats (*Macroderma*). The living *M. gigas* is a predator of small vertebrates, which it captures from the ground or perch. Prey are eaten in the roost caves by chewing through the pectoral region, manifested in the skeleton as extreme damage to the sternum (Boles unpubl. data); distal wings and legs are discarded. This is consistent with the elements that predominate at former *Macroderma*-accumulated sites at Riversleigh (carpometacarpus, tibiotarsus, tarsometatarsus). Unlike northern Australia today, where only a single species exists, Riversleigh is known to have supported many species of ghost bats during the Tertiary (Hand in press). Several sites have been identified as the remnants of *Macroderma* roost caves, such as the Miocene Gotham Site and the Pliocene Rackham's Roost Site.

PROBLEMS IN INTERPRETATION

There are several reasons why the Riversleigh birds do not offer the same depth of environmental data as living forms. Many specimens are yet to be studied. Ordinal level identification (Table 1) is frequently not fine enough for meaningful habitat inferences, especially for terrestrial species. There may be insufficient morphological differences between related forms occupying different habitats. Much of the biology of extinct groups remain unknown. Basic assumptions could be wrong; primary ones employed here are

that fossil birds had similar ecological characteristics to living counterparts and within a lineage more primitive species occur in rainforests, more derived ones in more open habitats.

PALAEOENVIRONMENT

The birds show that both aquatic and terrestrial habitats were prominent through the early to mid Miocene at Riversleigh. Because of the broad spectrum of wetland situations in which they occur, the cormorant, ducks and rail do not provide any clues to the detailed nature of these systems. Based on modern habitat preferences, the stork indicates shallow, slow moving, lacustrine situations somewhere in the area.

Several of the better taxonomically resolved specimens are consistent with a closed forest. The passerines *Orthonyx* and *Menura* belong to families which are today almost exclusively restricted to rainforest. Living halcyonid kingfishers occur through most Australian habitats; the Riversleigh form, however, is suggestive of more primitive, rainforest-inhabiting taxa.

Possible support for a more open habitat in some places comes from *Emuarius*. Its hindlimb proportions are thought to resemble those of *Dromaius novaehollandiae*, a highly cursorial animal. If the assumption can be made that the similarities in morphological proportions of the hindlimbs reflect similarities in function, this implies an advanced level of cursoriality in *Emuarius* as well.

The Pliocene environment of Riversleigh, based on Rackham's Roost site, was quite different from the Miocene. The Pliocene fossils are all small forms, mostly passerine but including a small extant parrot, *Melopsittacus undulatus*. This species is widespread, in arid and semiarid woodlands and scrublands, including the Riversleigh area. It requires proximity of water. Thus it suggests that Riversleigh in the Pliocene was probably very much like it is today.

The Riversleigh early to mid Miocene environment probably included shallow water at a number of different sites, with some surrounding rainforest and some more open forrests.

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A NEW OLIGOCENE-MIOCENE SPECIES OF *BURRAMYS* (MARSUPIALIA, BURRAMYIDAE) FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

J. BRAMMALL AND M. ARCHER

Brammall, J. & Archer, M. 1997 06 30: A new Oligocene-Miocene species of *Burramys* (Marsupialia, Burramyidae) from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 247-268. Brisbane. ISSN 0079-8835

Burramys is abundant in the Oligocene-Miocene at Riversleigh, northwestern Queensland. *Burramys brutyi* sp. nov. is represented by over 150 dentary and maxillary fragments and isolated teeth from 22 sites. *Burramys* appears to be morphologically conservative, with only minor metrical variation between specimens of *B. brutyi* from different sites and relatively few features distinguishing Miocene, Pliocene and Recent species. Phylogenetic analyses suggest that *B. brutyi* is the plesiomorphic sister-group to all other species of *Burramys*, with *B. wakefieldi* sister-group to the clade comprising *B. triradiatus* and *B. parvus*. □
Burramyidae, Burramys brutyi, Riversleigh, Oligocene, Miocene.

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Burramys was represented only by Pleistocene fossils of *B. parvus* from Wombeyan Caves, NSW (Broom, 1896) and Pyramids Cave, Victoria (Wakefield, 1960) until 1966 when the Mountain Pygmy-possum, *B. parvus*, was discovered alive at Mount Hotham, Victoria (Anon., 1966; Warneke, 1967). Two more fossil species of *Burramys* have been identified: early Pliocene *B. triradiatus* from Hamilton, Victoria (Turnbull et al., 1987) and *B. wakefieldi* from late Oligocene (Woodburne et al., 1993) Ngama Local Fauna, South Australia (Pledge, 1987). Discovery of Miocene *Burramys* at Riversleigh extends the geographic range far north and provides the first sizeable Tertiary sample (150 specimens). A metric analysis of this sample aims to determine taxa present and to assess variation. *Burramys brutyi* sp. nov. is used as the basis for an evaluation of intrageneric phylogenetics of *Burramys*.

Dental homology follows Flower (1867) for premolar numbering and Lockett (1993) for premolar/molar boundary and molar number. Tooth positions given without super- or subscript numbers refer to both upper and lower teeth; thus M^1 and M_1 are individual teeth but $M4$ refers to both. Molar cusp nomenclature follows Archer (1984) not Pledge (1987). Pledge's paraconid is our protoconid; his protoconid is not recognised.

Higher systematic nomenclature follows Aplin & Archer (1987). System nomenclature is based on Archer et al. (1989) and Creaser (1997). Material referred to is housed in the Queensland Museum, Brisbane (QMF) or Museum of Victoria, Melbourne, (NMVP). Measurements in millimetres (mm) are to the nearest 0.01 mm using a Wild MMS235 Digital Length-Measuring Set

attached to a Wild M5A stereomicroscope. Molar lengths and widths and molar row lengths were measured as the maximum dimensions of the enamel-covered crown(s) with the teeth in occlusal view, with lengths taken along the anteroposterior axis of the tooth and widths measured perpendicular to that axis. For P_3 in dorsal view and P^3 in ventral view, maximum length was measured parallel to the apical blade edge, and anterior, posterior and maximum widths were measured perpendicular to the blade edge; buccal and lingual heights were measured from the base of the enamel at the saddle between the roots, to the median apical edge, parallel to the posterior edge of the tooth. Statistical analyses were performed using SYSTAT and Kaleidagraph data analysis and graphics applications.

METRIC ANALYSIS

Despite overall uniformity, Riversleigh *Burramys* material shows some variation in relative and absolute premolar and molar sizes. Metric analysis of dental features attempted to identify patterns which might indicate sexual dimorphism, specific or subspecific separation or differentiation of populations from different sites. Univariate and bivariate distributions and principal components analysis were employed.

Cheektooth dimensions (Table 1) for Recent *B. parvus* populations refer to left dentition except where the right dentition was more complete. Standard error (SE) is used rather than standard deviation (SD) because it better indicates reliability of the mean estimate. The coefficient of variation (CV) = SD divided by mean $\times 100$.

TABLE 1. Cheektooth dimensions of *Burramys* species. Results given as: Mean \pm Standard Error (No. Specimens) Coefficient of Variation (CV%). CV not given where $n \leq 2$. L = length, AW = anterior width, PW = posterior width, MW = maximum width, LH = lingual height, BH = buccal height.

	Riversleigh <i>Burramys</i>		<i>B. wakefieldi</i>		<i>B. triradiatus</i>		<i>B. parvus</i>	
		CV		CV		CV		CV
<i>Lower teeth</i>								
P ₃ L	1.81 \pm 0.01 (38)	4.00	1.64	(1)	2.58 \pm 0.05 (4)	3.68	2.17 \pm 0.01 (21)	1.96
P ₃ AW	1.03 \pm 0.01 (38)	8.21	0.86	(1)	1.04 \pm 0.01 (4)	1.85	0.85 \pm 0.02 (21)	10.51
P ₃ PW	1.22 \pm 0.01 (38)	5.07	1.22	(1)	1.49 \pm 0.06 (4)	7.96	1.32 \pm 0.01 (21)	4.11
P ₃ MW	1.27 \pm 0.01 (29)	5.58	1.22	(1)	1.67 \pm 0.06 (4)	6.61	1.39 \pm 0.02 (21)	4.79
P ₃ LH	1.44 \pm 0.01 (37)	5.25	1.29	(1)	2.02 \pm 0.04 (4)	3.73	1.92 \pm 0.01 (19)	3.23
P ₃ BH	1.73 \pm 0.02 (37)	5.64	1.51	(1)	2.44 \pm 0.05 (4)	3.98	2.22 \pm 0.02 (20)	3.05
M ₁ L	1.24 \pm 0.01 (32)	3.71	1.21	(1)	-	-	1.57 \pm 0.01 (21)	2.02
M ₁ AW	0.78 \pm 0.01 (32)	7.89	0.86	(1)	-	-	1.00 \pm 0.01 (21)	4.23
M ₁ PW	0.95 \pm 0.01 (32)	5.80	0.97	(1)	-	-	1.25 \pm 0.01 (21)	3.60
M ₂ L	1.09 \pm 0.01 (32)	3.72	-	-	1.55	(1)	1.57 \pm 0.01 (21)	1.97
M ₂ AW	0.88 \pm 0.01 (34)	5.55	-	-	1.23	(1)	1.21 \pm 0.01 (21)	2.03
M ₂ PW	0.96 \pm 0.01 (34)	5.67	-	-	1.32	(1)	1.32 \pm 0.01 (21)	1.90
M ₃ L	0.93 \pm 0.02 (10)	6.48	-	-	1.32 \pm 0.04 (2)	4.29	1.23 \pm 0.01 (19)	1.84
M ₃ AW	0.84 \pm 0.01 (10)	4.46	-	-	1.13 \pm 0.00 (2)	0.00	1.06 \pm 0.01 (19)	2.25
M ₃ PW	0.85 \pm 0.02 (10)	6.13	-	-	1.17 \pm 0.01 (2)	0.61	1.07 \pm 0.01 (19)	2.76
M ₄ L	0.66	(1)	-	-	-	-	0.68 \pm 0.01 (14)	5.88
M ₄ AW	0.64	(1)	-	-	-	-	0.66 \pm 0.01 (14)	6.83
M ₄ PW	0.50	(1)	-	-	-	-	0.52 \pm 0.01 (14)	7.82
M ₁ -2	2.30 \pm 0.02 (27)	3.37	-	-	-	-	3.13 \pm 0.01 (21)	1.96
M ₁ -3	3.24 \pm 0.05 (8)	3.91	-	-	-	-	4.34 \pm 0.01 (19)	1.34
M ₁ -4	3.83	(1)	-	-	-	-	4.93 \pm 0.02 (14)	1.29
<i>Upper teeth</i>								
p ₃ L	2.01 \pm 0.02 (17)	4.89	-	-	2.59 \pm 0.02 (2)	1.09	2.27 \pm 0.01 (19)	2.60
p ₃ AW	0.93 \pm 0.01 (17)	4.32	-	-	0.91 \pm 0.02 (2)	2.32	0.75 \pm 0.02 (19)	10.39
p ₃ PW	1.20 \pm 0.01 (17)	4.93	-	-	1.63 \pm 0.05 (2)	4.79	1.13 \pm 0.01 (19)	3.82
p ₃ MW	1.25 \pm 0.01 (17)	4.41	-	-	1.63 \pm 0.05 (2)	4.79	1.24 \pm 0.01 (19)	2.44
p ₃ LH	1.58 \pm 0.02 (17)	4.67	-	-	2.32 \pm 0.02 (2)	1.22	1.92 \pm 0.01 (16)	2.76
p ₃ BH	1.65 \pm 0.02 (17)	4.44	-	-	2.16 \pm 0.01 (2)	0.98	2.06 \pm 0.02 (18)	3.08
M ₁ ¹ L	1.12 \pm 0.02 (14)	4.86	-	-	-	-	1.51 \pm 0.01 (19)	1.94
M ₁ ¹ AW	1.16 \pm 0.02 (14)	5.25	-	-	-	-	1.40 \pm 0.02 (19)	7.08
M ₁ ¹ PW	1.17 \pm 0.01 (14)	4.14	-	-	-	-	1.45 \pm 0.01 (19)	4.01
M ₁ ¹ MW	1.39 \pm 0.01 (14)	3.90	-	-	-	-	1.68 \pm 0.01 (18)	2.77
M ₂ ² L	0.98 \pm 0.01 (8)	3.45	-	-	1.22	(1)	1.45 \pm 0.01 (19)	1.53
M ₂ ² AW	1.16 \pm 0.01 (8)	2.84	-	-	1.34	(1)	1.56 \pm 0.01 (19)	2.20
M ₂ ² PW	0.93 \pm 0.01 (8)	2.40	-	-	1.10	(1)	1.27 \pm 0.01 (19)	3.37
M ₃ ³ L	0.86 \pm 0.03 (3)	6.43	-	-	-	-	1.09 \pm 0.02 (18)	8.17
M ₃ ³ AW	0.93 \pm 0.02 (3)	2.84	-	-	-	-	1.19 \pm 0.03 (18)	10.83
M ₃ ³ PW	0.72 \pm 0.03 (3)	7.86	-	-	-	-	0.88 \pm 0.02 (18)	10.71
M ₄ ⁴ L	0.67 \pm 0.02 (3)	5.68	-	-	-	-	0.77 \pm 0.01 (13)	4.86
M ₄ ⁴ AW	0.71 \pm 0.02 (3)	4.97	-	-	-	-	0.74 \pm 0.02 (13)	8.81
M ₄ ⁴ PW	0.46 \pm 0.03 (3)	10.80	-	-	-	-	0.51 \pm 0.01 (13)	9.49
M ₁ ¹ -2	2.11 \pm 0.03 (8)	3.40	-	-	-	-	2.96 \pm 0.01 (19)	1.85
M ₁ ¹ -3	2.98 \pm 0.08 (3)	4.55	-	-	-	-	4.07 \pm 0.02 (18)	1.63
M ₁ ¹ -4	3.55 \pm 0.03 (3)	1.33	-	-	-	-	4.77 \pm 0.03 (13)	1.86

CV is less than 11 throughout and usually less than 6 (Table 1). Following Simpson et al. (1960), this degree of variation indicates an unmixed sample, although Gingerich (1974) cautions against uncritical application of this absolute CV criterion and recommends greater emphasis on relative variabilities of different teeth. In approx-

imately 80% of measurements *B. parvus* has a lower CV than the Riversleigh sample, but the interspecific differences in CV are generally not great. CVs for *B. triradiatus* fall within approximately the same ranges as those for the Riversleigh and Recent specimens, but are derived from very few specimens and are therefore

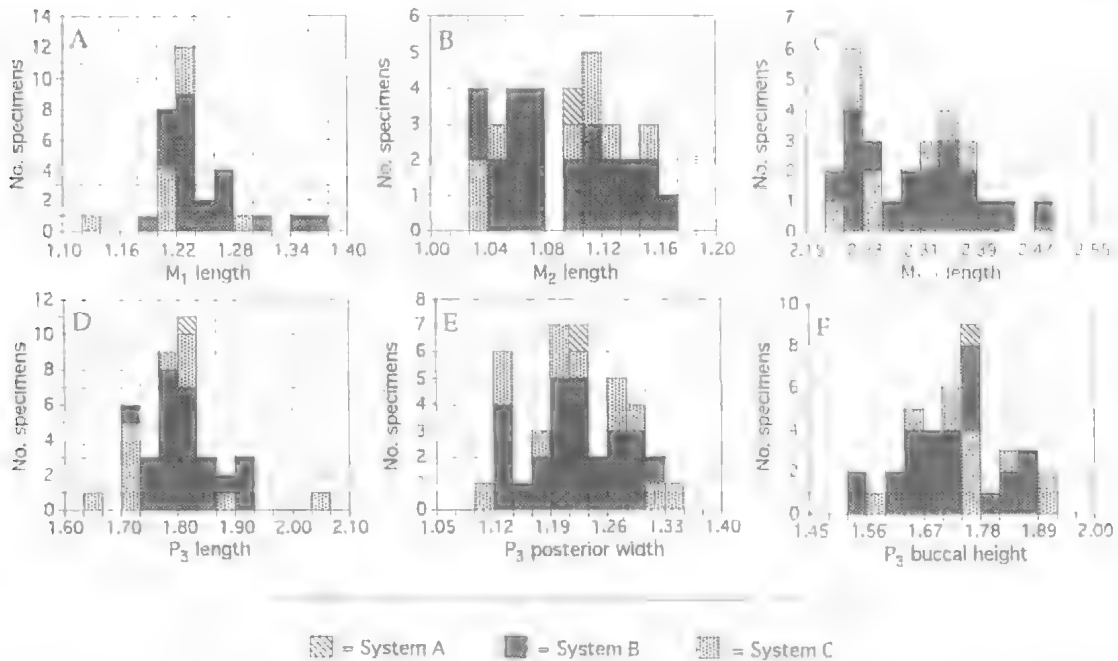


FIG. 1. Frequency histograms for some lower tooth measurements of Riversleigh *Burramys* specimens. All measurements in mm.

not considered reliable. Total variation (as indicated by CVs) suggests 1 species of *Burramys* in the Riversleigh sample spanning greater variation than the sample of Recent *B. parvus*.

Where variation between taxa is small (as is likely with small-bodied taxa), it may be obscured by epigenetic morphological variation, by tooth wear or by measurement error; metric differences between closely related taxa are most likely to be detected by examining structures with the lowest levels of such variation. M₂, in the centre of the P₃-M₄ tooth row, is in that sense the most functionally integrated of these teeth; it may therefore be expected to be least variable (Gingerich, 1974). Similarly, total molar row lengths may be more tightly controlled than the lengths of individual molars. M₂ dimensions and molar row measurements (including partial molar row measurements such as M₁₋₂ length) are generally the least variable measurements in *B. parvus* and the Riversleigh sample; P₃ length is also relatively constant (Table 1). Thus analysis of the Riversleigh sample was focused on P₃ and M₁₋₂, although all other measurements were examined.

Frequency histograms for some measurements are bimodal, while others are either unimodal or perhaps incipiently bimodal. M₁₋₂ length (Fig.

1C), with CV=3.37 is bimodal. M₂ length (Fig. 1B; CV=3.72) and P₃ buccal height (Fig. 1F; CV=5.64) are considered bimodal, though not with certainty. M₁ length (Fig. 1A; CV=3.71) may represent a bimodal distribution but could equally be a sample from a unimodal, normal distribution; P₃ length (Fig. 1D; CV=4.00) and P₃ posterior width (Fig. 1E; CV=5.07) distributions could each be described either as having 2 or 3 peaks, or as representing single normal distributions. Kolmogorov-Smirnov Lilliefors tests indicate that some of the univariate distributions differ significantly from normal (Table 2) and comparison with Table 1 shows that these include several with low variation. Thus univariate frequency distributions hint that the sample represents more than one population, but do not provide a basis for subdivision.

Bivariate plots (Fig. 2) suggest no clear divisions other than those evident in the univariate distributions, such as the apparent bimodality of M₂ length (Fig. 1B, 2B). They show that specimens from Systems B and C have overlapping distributions, but that for some measurements, specimens from System C sites are, on average, smaller than specimens from System B sites. This is so for M₁ length and P₃ length (Fig. 2A, 2C) and to a lesser extent for M₂ length (Fig. 2B).

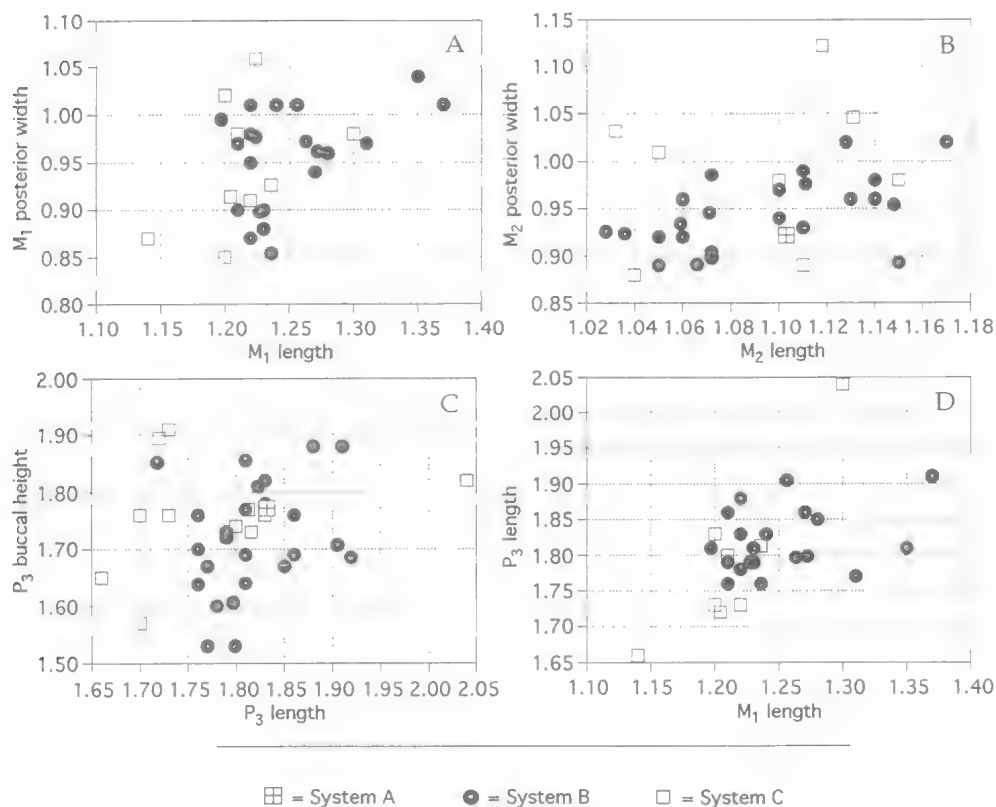


FIG. 2. Bivariate plots for some lower tooth measurements of Riversleigh *Burramys* specimens. All measurements in mm.

TABLE 2. Column 1, Kolmogorov-Smirnov Lilliefors tests for normality. Probability (P) values below 0.05 indicate a difference from normality significant at the 95% level. Columns 2 and 3, mean values for Systems B and C respectively. Column 4, Students t-tests; P indicates a significant difference between Systems B and C. Abbreviations as for Table 1.

	Lilliefors Test (P)	Mean - System B	Mean - System C	T-test (P)
P ₃ L	0.088	1.82	1.79	0.266
P ₃ AW	0.175	1.03	1.05	0.474
P ₃ PW	0.455	1.22	1.22	0.928
P ₃ MW	0.678	1.26	1.29	0.211
P ₃ LH	0.215	1.43	1.44	0.923
P ₃ BH	0.904	1.72	1.76	0.254
M ₁ L	0.002	1.25	1.21	0.071
M ₁ AW	0.193	0.79	0.76	0.268
M ₁ PW	0.072	0.96	0.95	0.625
M ₂ L	0.009	1.09	1.09	0.903
M ₂ AW	0.009	0.87	0.91	0.041
M ₂ PW	0.585	0.95	0.98	0.111
M ₃ L	0.593	0.93	0.98	0.458
M ₃ AW	0.177	0.85	0.81	0.394
M ₃ PW	0.038	0.85	0.81	0.458
M ₁₋₂	0.054	2.32	2.27	0.226
M ₁₋₃	0.001	3.25	3.16	0.529

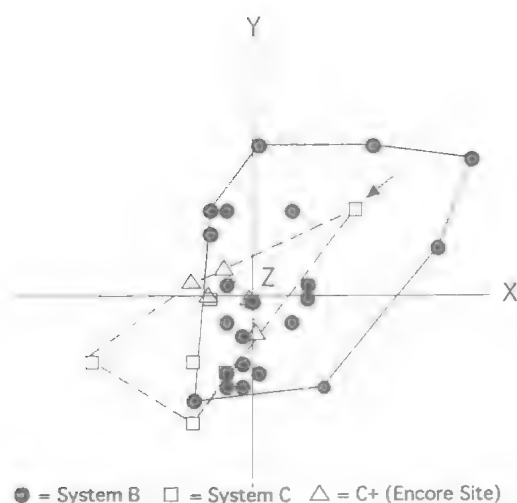


FIG. 3. Specimens of *Burramys* from various sites at Riversleigh plotted on principal component axes obtained using 11 measurements from P_3 and M_{1-2} . Eigenvectors recorded in Table 3. X = first principal axis, Y = second principal axis, Z (perpendicular to page) = third principal axis. Solid line encloses specimens from System B sites. Dashed line encloses specimens from System C sites, including Encore Site. Dotted line excludes from System C 'aberrant' specimen QMF30104, indicated by arrow.

but appears not to be the case for P_3 buccal height (Figs 2C). M_2 posterior width shows the opposite trend (Fig. 2B), whereby System C specimens are on average larger than System B specimens. Student's t-tests show these differences to be non-significant at the 95% level (Table 2), but a principal components analysis employing dimensions of P_3 and M_{1-2} (Fig. 3, Table 3) confirms

that total variation is explained partly by System C specimens being smaller than system B specimens. Eigenvectors for component 1 are all positive (Table 3), indicating that this is a general 'size component'; specimens scoring high on the first component (i.e. falling further towards the positive, or right-hand side of the X-axis in Fig. 3) are larger than those to the left. Although there is considerable overlap between Systems B and C, the centre of mass of the System B distribution is further to the right than that for System C.

Specimens from Encore site (younger than System C, ?early late Miocene) cluster at one extreme of the System C distribution, with the exception of a single large aberrant specimen QMF30104 from Gag Site (Fig. 3). In the System B-System C continuum (Fig. 3) the cluster of Encore Site specimens falls on the 'older' (System B) end of the System C spectrum.

Despite the apparent trend of mean difference between specimens from Systems B and C, specimens from both Systems are present in each of the apparent peaks of the univariate distributions (Fig. 1A-F). This suggests that the underlying structure of the sample is not simply anagenetic change tracked from the older System B sites to younger System C sites, though such may have occurred. The bimodality of several of the frequency histograms may reflect sexual dimorphism and/or 2 roughly contemporaneous taxa. This suggestion is also supported by data plotted against sites arranged in estimated stratigraphic order (Fig. 4A-F.) Although samples from individual sites are inadequate to compare within- and between-site variation statistically, variation between sites is only a little greater than that within Upper site, provenance of the largest sample. Caution is therefore necessary when interpreting apparent between- or across-site trends (such

TABLE 3. Results of principal components analysis using 11 measurements of P_3 and M_{1-2} of *Burramys* specimens from Riversleigh. Abbreviations as for Table 1.

Component:	1	2	3	4	5	6	7	8	9	10	11
Eigen Value:	4.971	2.177	1.179	0.803	0.638	0.497	0.336	0.230	0.097	0.049	0.022
Percent	45.194	19.790	10.716	7.299	5.801	4.519	3.056	2.092	0.883	0.447	0.203
Cumulative percent	45.194	64.984	75.699	82.998	88.799	93.318	96.374	98.466	99.350	99.797	100.000
Eigenvectors:											
M_1L	0.304	-0.297	0.076	0.510	-0.328	0.126	0.172	-0.398	0.088	0.304	0.376
M_1AW	0.323	-0.178	-0.285	0.040	0.397	-0.500	0.507	-0.020	-0.033	0.188	-0.282
M_1PW	0.387	0.005	-0.265	-0.199	0.131	-0.356	-0.414	0.033	0.006	-0.188	0.623
M_2L	0.209	-0.489	0.152	-0.278	0.293	0.353	-0.240	0.294	0.277	0.426	-0.060
M_2AW	0.203	0.368	-0.472	-0.204	0.053	0.535	0.381	0.193	-0.138	0.152	0.213
M_2PW	0.362	0.150	-0.390	0.127	-0.107	0.168	-0.380	-0.299	0.338	-0.150	-0.518
M_{1-2}	0.324	-0.403	0.142	-0.106	0.051	0.290	0.099	-0.117	-0.507	-0.567	-0.111
P_3L	0.363	0.015	0.179	0.117	0.512	-0.184	0.118	0.666	0.169	-0.164	-0.117
P_3PW	0.188	0.344	0.215	0.617	0.510	0.146	-0.184	0.248	-0.204	0.018	0.016
P_3LH	0.322	0.303	0.313	-0.303	-0.219	-0.159	-0.198	-0.191	-0.468	0.461	-0.187
P_3BH	0.250	0.332	0.498	-0.258	0.211	0.056	0.313	-0.267	0.486	0.218	0.112

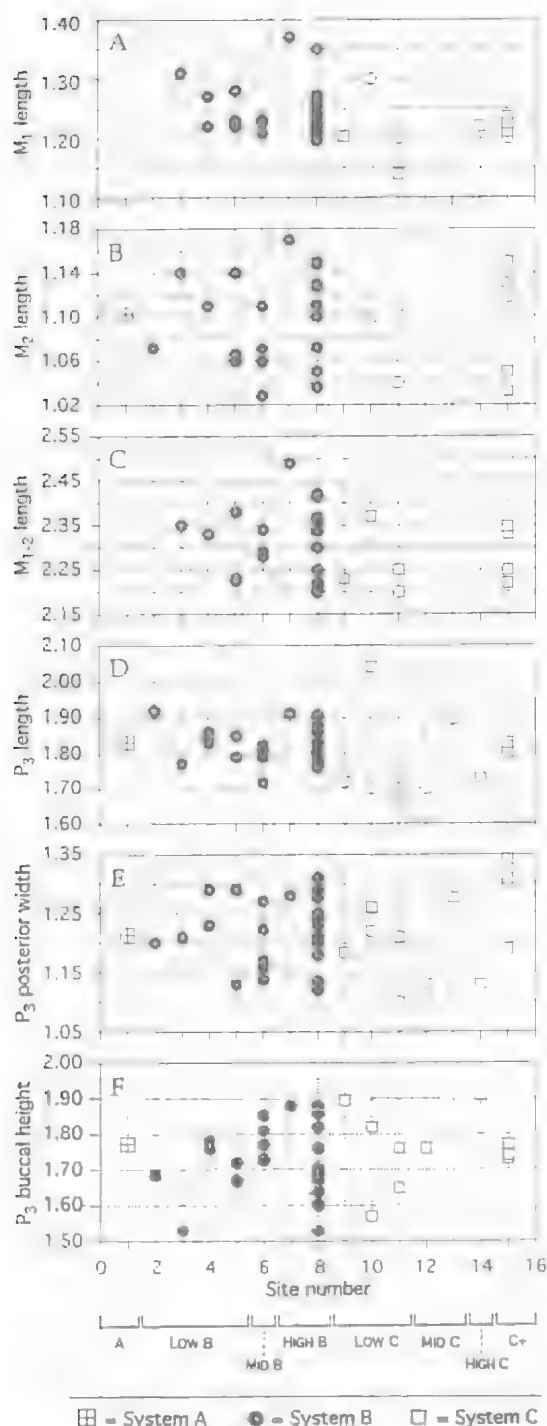


FIG. 4. Riversleigh *Burramys*: size measures against sites in stratigraphic sequence (Archer et al., 1989). Distances on horizontal axis arbitrary. Sites: 1=White Hunter; 2=Creaser's Ramparts; 3=Outasite; 4=RSO;

as size decline over time) as being significant. Although site 8 (Fig.4) includes Ten Bags Site, Mike's Potato Patch and Upper Site, most specimens are from Upper Site and these span the range of variation at site 8.

If two morphotypes are present they are both represented in Upper Site (Fig.4). Muirhead (1994) demonstrated size-guilding comparable to that in Recent mammal communities among 7 Upper Site bandicoot species separated on size; this is possibly due to competitive displacement of taxa that eat size-variable foods such as seeds or insects within a single community. Thus, Upper Site probably represents a single diverse community and the 2 morphotypes of *Burramys* could be sexual dimorphs or sympatric taxa. We reject sympatry because of morphological consistency of specimens falling near the peaks in the M_{1+2} length distribution; the size difference between those peaks is too small (Roth, 1981) to represent 2 species in different niches at the same level of a food web. The ratio of the second peak to the first (Fig. 1A-C) is 1.06, short of the often-cited cutoff value of 1.3. (Roth (1981) showed that the 'constant ratio rule' is empirically unsubstantiated, but suggested that character displacement is unlikely to be indicated by ratio values lower than 1.3.)

Challenging the likelihood of either sexual dimorphism or sympatry is the fact that some specimens are in the higher peak of apparently bimodal distributions for some measurements, but the lower peak for others; whereas other specimens remain in one peak or the other for all or most measurements. There appears to be no combination of features that can be used to subdivide the sample; this is supported by the multivariate analysis (Fig. 3) which fails to divide the sample. A general trend to declining size through Systems B and C (Figs 2,3,4A,C) is evident, but some Encore Site specimens suggest reversal of the trend.

SUMMARY

Riversleigh *Burramys* specimens may represent two populations. Patterns of variation also suggest a cline of decreasing size through time; however, small sample sizes and uncertainty of relative ages limit the reliability of this observa-

5=Wayne's Wok; 6=Camel Sputum, Neville's Garden and Dirk's Towers; 7=Inabeyance; 8=Ten Bags, Mike's Potato Patch and Upper Site; 9=Kangaroo Jaw; 10=Gag; 11=Last Minute; 12=Main Site; 13= Jim's Jaw; 14=Wang; 15=Encore.

tion. If two populations have been sampled, magnitude and distribution of variation suggest that these are males and females of 1 species. Extant populations of *B. parvus* are not dentally dimorphic (Brammall, unpubl.), but their alpine habitat is far removed from the Miocene rainforest environment at Riversleigh (Archer et al., 1989, 1991) so it is not possible to infer that Recent and Miocene *Burramys* share population structures. We recognise a single new species.

SYSTEMATIC PALAEONTOLOGY

Class Mammalia Linnaeus, 1758
 Supercohort Marsupialia Illiger, 1811
 Order Diprotodontia Owen, 1866
 Superfamily Burramyoidea Broom, 1898
 Family Burramyidae Broom, 1898

Burramys Broom, 1896

Burramys brutyi sp. nov.

(Figs 5-9; Tables 1,4)

ETYMOLOGY For the late Arthur Bruty who, together with his daughter Elaine Clarke, helped collect many specimens and discovered Bruty & the Beast Site on the Gag Plateau.

MATERIAL. Holotype QMF30102 (Fig. 5), a left dentary (DEN) with I₁, P₁₋₃, M₁₋₂ and alveoli for I₂ and M₃₋₄. The tip of I₁ is missing, as are the condylar, angular and coronoid processes. Paratypes QMF30176 (Fig. 6), R DEN with P₂₋₃, M₁₋₄, broken anterior to P₂ and missing the ascending ramus and condylar, angular and coronoid processes, QMF30091 (Fig. 7), L maxilla with P₂₋₃, M₁₋₄ and palate medial to cheekteeth. Types from early to mid Miocene Upper Site on Goddell Hill, DSite Plateau.

Other material: SYSTEM A - White Hunter Site, QMF23344, RM₂; QMF23500, DEN with RP₃, SYSTEM B - Camel Sputum Site, QMF20732, DEN with RM₁, P₃; QMF20735, R DEN; QMF20736, LM₂; QMF30090, maxilla with LP₂₋₃, M₁; QMF30107, DEN with LI₁, P₂₋₃, M₁₋₂; QMF30110, DEN with RI₁, P₂₋₃, M₁₋₂. Inabeyance Site: QMF30079, DEN with LP₃, M₁₋₃. Mike's Potato Patch Site: QMF20759, DEN with LM₂; QMF20760, LM₁; QMF20761, P₃ or P₄. Neville's Garden Site: QMF20718, DEN with RP₃, M₁; QMF20748, LM₂; QMF20902, DEN with RI₁, P₄, M₁; QMF23349, DEN with LP₃, M₁₋₂; QMF23376, DEN with RP₃, M₁; QMF23511, DEN with RP₃; QMF24261, maxilla with RP₂₋₃; QMF30089, maxilla with RP₂₋₃, M₁₋₂; QMF30092, maxilla with RP₂₋₃, M₁₋₄; QMF30113, DEN with RP₃, M₁; QMF30114, LP₃; QMF30132, DEN with LP₃, M₁₋₂; QMF30271, RM₃; Outasite: QMF20769, L DEN; QMF30080, DEN with LI₁, P₃, M₁₋₃. RSO Site: QMF30081, DEN

with LP₃, M₁₋₃; QMF30084, DEN with RI₁, P₃, M₁; QMF30094, maxilla with RP₂; QMF30140, LP₃; QMF30141, LP₃; QMF30142, RP₃. Ten Bags Site, QMF23502, DEN with LP₃, M₁. Upper Site, QMF20774, DEN with RI₁; QMF20775, DEN with LI₁, P₃; QMF20776, DEN with RP₃; QMF20777, DEN with RM₂; QMF20785, maxilla with RM₁₋₃; QMF20786, DEN with LM₁₋₃, P₃; QMF20787, maxilla with LM₁, P₂₋₃; QMF20788, maxilla with LM₁; QMF30082, DEN with LP₃, M₁₋₂; QMF30083, DEN with RP₂₋₃, M₁₋₂; QMF30085, DEN with LI₁, P₃, M₁; QMF30086, DEN with RI₁, P₂₋₃, M₁₋₂; QMF30087, maxilla with LP₂₋₃; QMF30088, maxilla with LP₂₋₃; QMF30091, maxilla with LP₂₋₃, M₁₋₄; QMF30095, maxilla with RP₃, M₁₋₂; QMF30096, maxilla with LP₃; QMF30097, maxilla with RP₃; QMF30098, maxilla with RP₃, M₁; QMF30099, maxilla with RP₃; QMF30101, maxilla with LP₂₋₃, M₁₋₂; QMF30102, DEN with LI₁, P₁₋₃, M₁₋₂; QMF30103, maxilla with LP₃, M₁; QMF30106, DEN with RI₁, P₂₋₃; QMF30111, DEN with LI₁, P₂₋₃, M₁; QMF30112, DEN with RI₁, P₃; QMF30117, DEN with RP₃, M₁₋₂; QMF30118, DEN with RI₁, P₃, M₁; QMF30119, DEN with RM₂₋₃; QMF30120, DEN with LP₃, M₁₋₂; QMF30121, DEN with LI₁, P₃; QMF30122, DEN with LI₁, P₃; QMF30123, DEN with LP₃, M₁₋₂; QMF30124, DEN with RP₃, M₁₋₃; QMF30125, DEN with RP₃, M₁; QMF30127, DEN with LI₁, P₃; QMF30128, DEN with RP₃; QMF30129, R DEN; QMF30130, 30131, L DEN; QMF30133, DEN with RP₃, M₁₋₂; QMF30138, maxilla with LP₂; QMF30139, RP₂; QMF30146, 30148, 30149, 30152 LP₃; QMF30147, 30150, 30154, 30155, 30179, 30182 LP₃; QMF30151, 30153, 30174, 30180, 30184 RP₃; QMF30160, LM₂; QMF30164-30167, LM₁; QMF30168, 30173, 30177 RM₁; QMF30176, DEN with RP₂₋₃, M₁₋₄; QMF30181, 30183 RP₃; QMF30185, 30190 RM₃; QMF30186, RM₂; QMF30187, LI₁; QMF30188, RI₁; QMF30189, RM₂. Wayne's Wok Site: QMF20725, maxilla with RP₃; QMF20726, maxilla with RM₁₋₂; QMF20737, maxillary fragment with RP₃; QMF20738, DEN with RM₁; QMF20744, DEN with RM₁, P₃; QMF20745, DEN with LM₂₋₃; QMF20746, DEN with RM₁₋₂; QMF22816, maxilla with RP₂₋₃, M₁₋₄; QMF30108, DEN with RP₂₋₃, M₁₋₂; QMF30136, DEN with RI₁, P₃, M₁. Wayne's Wok 2 Site: QMF30100, DEN with RI₁, P₃, M₁₋₃; QMF30175, LP₃. SYSTEM B OR C - Cleft of Ages 1 Site: QMF20905, R DEN, Cleft of Ages 2A Site: QMF22772, maxilla with RP₃, M₁. Cleft of Ages 4 Site: QMF20767, RP₃; QMF20835, RP₃; QMF20836, RP₃; QMF23200, RP₃. SYSTEM C - Encore Site: QMF20752, LM₃; QMF20753, LP₃; QMF20754, LM₁; QMF20904, DEN with RM₁₋₂, P₂₋₃; QMF23462, DEN with RM₁₋₂, P₃; QMF24354, DEN with LM₁₋₂; QMF24424, DEN with LM₁; QMF24426, DEN with LI₁, P₃, M₂; QMF24552, RP₃; QMF24727, DEN with LI₁, P₃, M₁₋₂. Gag Site: QMF30078, DEN with RP₃; QMF30093, maxilla with LP₃; QMF30104, DEN with LI₁, M₁₋₂, P₃; QMF30134, L DEN; QMF30135, DEN with LP₃, M₁;

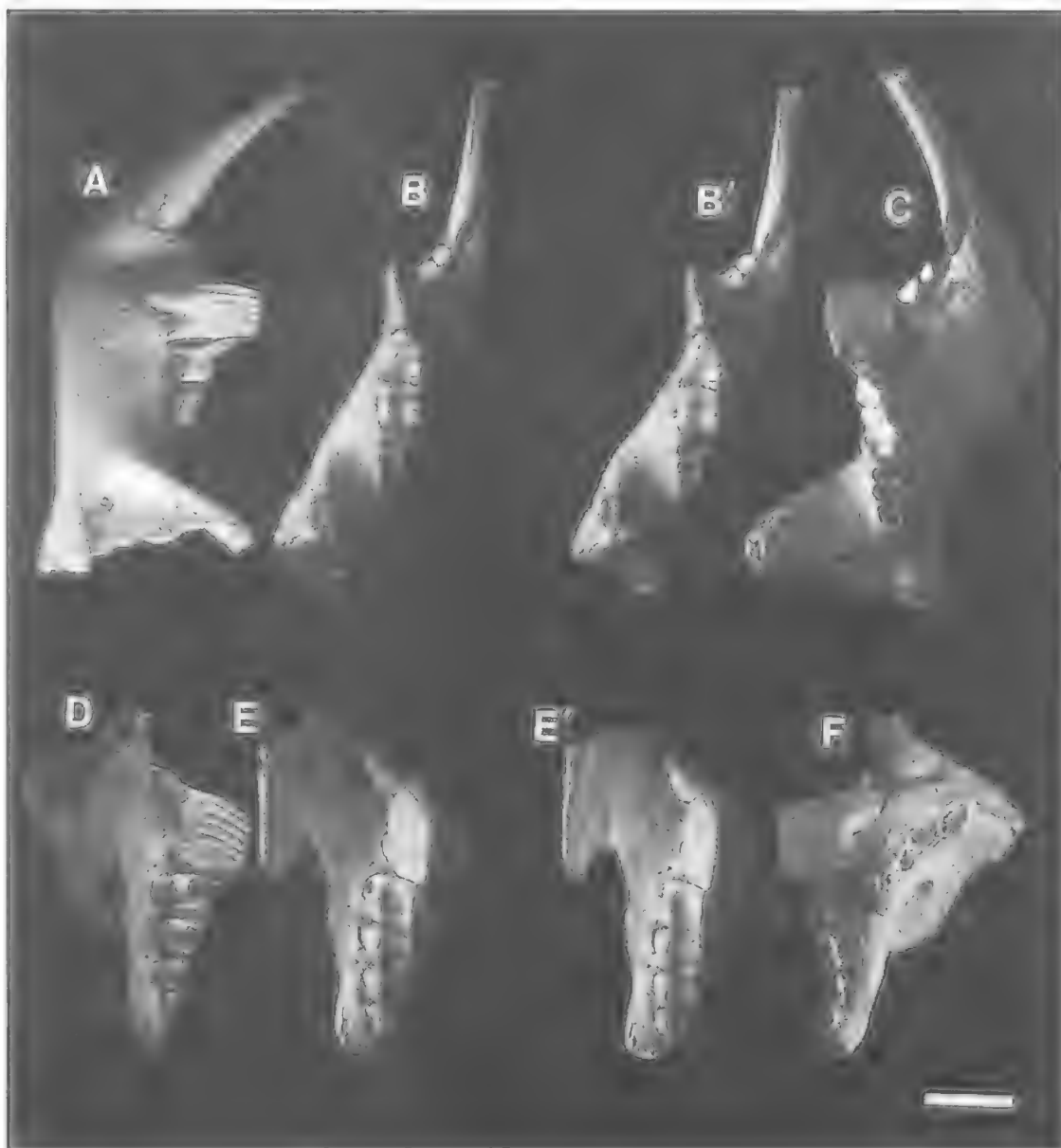


FIG. 5. A-C, *Burrumys brutyi* n. sp. holotype QMF30102. Left dentary with I₁ P₂₋₃ M₁₋₂ in (A) buccal, (B-B') occlusal stereopair and (C) lingual views. D-F, *Burrumys brutyi* paratype QMF30091. Left maxilla with P₂₋₃ M₁₋₄ in (D) buccal, (E-E') occlusal stereopair and (F) lingual views. Scale = 2mm.

QMF30137, LP³; QMF30156, LM₂; QMF30157, RM₁; QMF30158, RM₁; QMF30161, LM₃; QMF30170, RP₃; QMF30171, RP₃. Henk's Hollow Site: QMF30172, LP³. Jim's Jaw Site: QMF30178, DEN with RP₃. Kangaroo Jaw Site: QMF30115, DEN with RP₃, M₁₋₂. Last Minute Site: QMF30105, DEN with RI₁, M₁₋₃, P₂₋₃; QMF30116, DEN with RP₃, M₁₋₂; QMF30143, LP³; QMF30144, RP₃;

QMF30145, LP³ apical fragment; QMF30162, RM₃; QMF30163, RM₃; QMF30169, DEN with RP₃, M₁. Main Site: QMF30109, DEN with RP₃. Ringtail Site: QMF20756, RP₃; QMF20757, maxilla with RM₁₋₂, P₃. Wang Site: QMF20763, maxilla with LP³; QMF20766, DEN with RM₁, P₃; QMF30272, RP₃. AGE UNCERTAIN - Creaser's Ramparts Site: QMF20771, LP₃.



FIG. 6. *Burramys brutyi* paratype QMF30176: occlusal stereopair of right dentary fragment with P2-3 and M1-4. Scale = 2mm.

DIAGNOSIS. Differs from *B. triradiatus* and *B. parvus* in being smaller, in having upper and lower plagiaulaeoid P3 smaller and with fewer (5-6) cuspules and associated ridges and in having 2-rooted upper and lower M4. Dentary and maxilla more robust than in *B. parvus*, with smaller palatal vacuities, shorter I2-P2 interval and less reduced posterior molars. P3 with larger crown and larger posterior root than that of *B. wakefieldi* and diverging less from anteroposterior molar row axis. P1-2 double-rooted; single-rooted in *B. wakefieldi*. Distinguishable from *B. wakefieldi* and *B. parvus* by M1 cusp morphology: protoconid more lingual in *B. wakefieldi* than *B. parvus* or *B. brutyi*; metaconid more anterior in *B. parvus* than *B. brutyi* or *B. wakefieldi*.

COMPARATIVE DESCRIPTION. The dentary of *B. brutyi* is subequal to that of *B. wakefieldi* in size and shape. Both are more robust than that of *B. parvus* but slightly less so than that of *B. triradiatus*. The leading edge of the ascending ramus of *B. brutyi* is considerably more robust and rises at a steeper angle from the horizontal axis of the dentary than does that of *B. parvus*, but not quite as steeply as that of *B. triradiatus*. The I2-P2 interval is shorter in *B. brutyi* than in *B. parvus* but is not as short, relative to the length of the ramus, as that of *B. triradiatus*.

Lower dentition. I1 is long, slender and procumbent, with the tip curved upwards and slightly twisted. It is slightly less procumbent in *B. brutyi* than in *B. parvus*. The crown of I1 is basally about the same dorsoventral thickness in *B. brutyi* and

B. parvus but a little thicker in *B. triradiatus*. I1 of *B. brutyi* thins abruptly about half way along its exposed length, with the anterior half of the tooth being narrower than the posterior half. In lateral view I1 of *B. brutyi* is more curved than in the other species.

I2 has not been identified in *B. brutyi*, *B. wakefieldi* or *B. triradiatus*. In *B. parvus* I2 is small and single-rooted, inserting into a shallow alveolus directly behind the posterior alveolar margin of I1. Its crown inclines forward to overlie I1 posterobasally. In some specimens of *B. brutyi* there appears to be the remnant of a small alveolus in the fragile region between I1 and P1, suggesting a small, single-rooted I2.

P1 is small, 2-rooted and cap-like, the crown swelling beyond the roots in all directions. There is a minor ridge along the anteroposterior axis of the tooth, with the crown sloping away from the crest on each side towards the lingual and buccal margins respectively. In dorsal view it is almost circular in outline, being slightly wider than long. The crown does not extend as far beyond the roots posteriorly as it does in other directions. In *B. parvus* the crown is shorter and flatter than in *B. brutyi* and is also procumbent, rising slightly at its anterior end to overlie the posterior end of I2; it is ovoid in dorsal view (slightly longer anteroposteriorly) and its posterior end is reduced.

The anterior root of P1 inserts anterobuccal to the posterior root. The posterior alveolus is closer to the anterior alveolus of P2 than it is to the anterior alveolus of P1, inserting slightly lingually and anterior to the anterior alveolus of P2. The septum separating the posterior alveolus of P1 and the anterior alveolus of P2 frequently breaks down so that they form a single cavity. In some specimens, therefore, there may appear to be only three alveoli in the region which had been occupied by the 4 roots of P1 and P2. Even with the septum intact, the arrangement of alveoli might suggest that the posterior alveolus of P1 and the anterior alveolus of P2 belonged to the same tooth. Whereas in *B. brutyi* the alveoli of P1 and P2 are closely but unevenly spaced, in *B. parvus* the 5 alveoli of I2, P1 and P2 are evenly spaced and in the adult animal there is a small gap between P1 and P2 (in subadult or younger animals the teeth are closer together).

P2 is similar in shape but a little larger than P1. The slight anteroposterior crest lies at an angle (lingual posteriorly) across the alveolar margins, directly above an imaginary line joining the centres of the P2 alveoli. Posteriorly the crown extends beyond and rises above the root

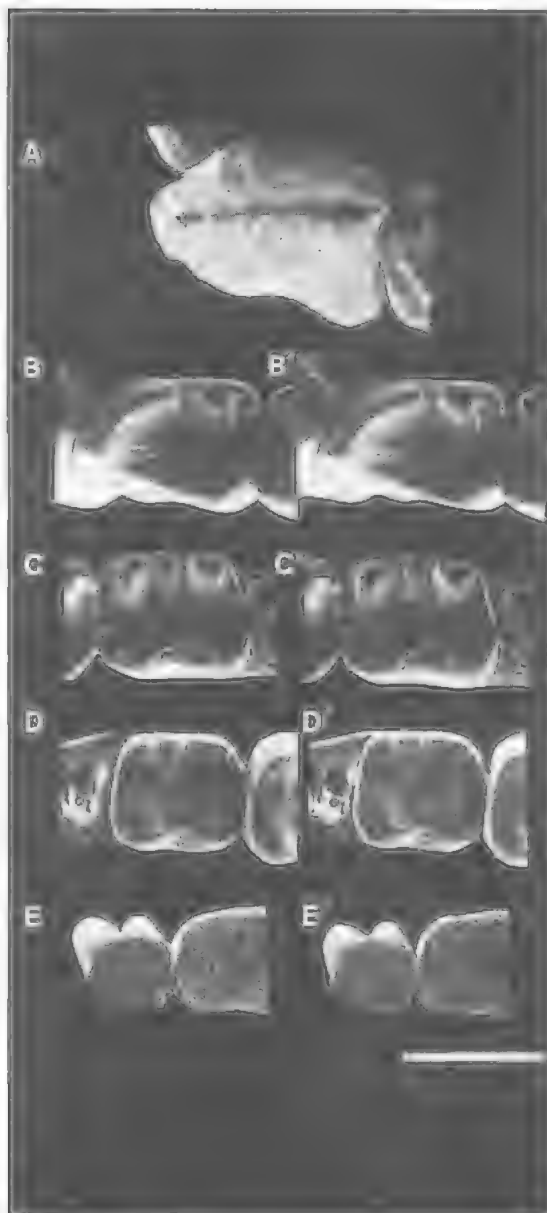


FIG. 7. Lower cheekteeth of *B. brutyi* in occlusal view. A-C, QMF 30102. A, LP₃. B-B', LM₁. C-C', LM₂. D-D' RM₃ of QMF30100. E-E', RM₄ of QMF30176. B-E stereopairs. Scale = 1mm.

terminating in a small cuspule and abutting P₃. Anteriorly, the crown extends slightly beyond the root. Lingually and buccally the crown swells out and falls away to a rounded point on each side. The buccal, ventral apex is slightly higher and more anteriorly located than the lingual apex, so

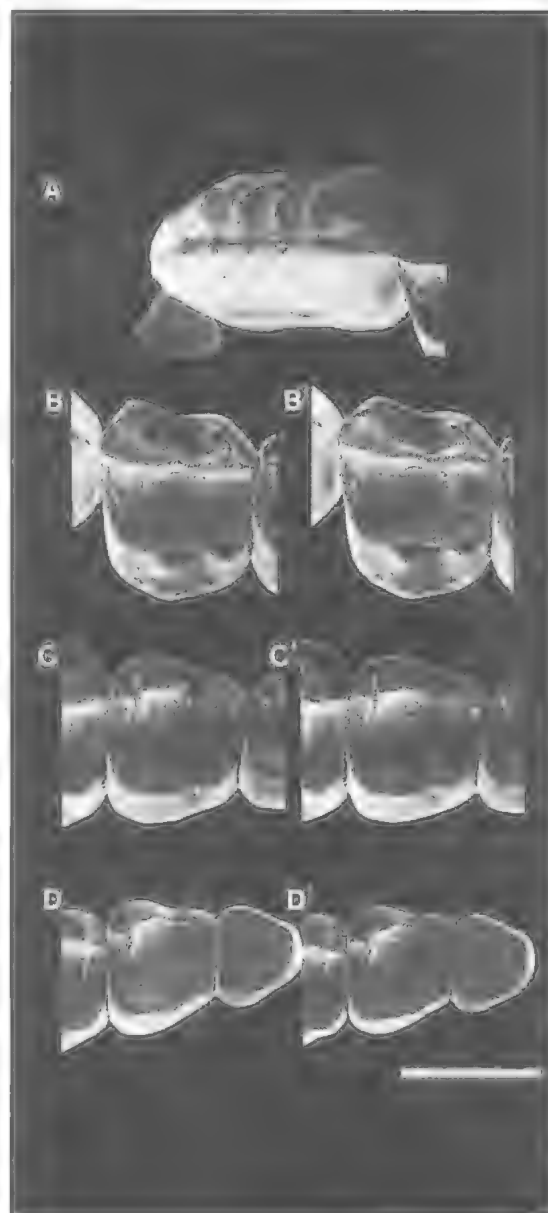


FIG. 8. Left upper cheekteeth of *B. brutyi* paratype QMF30091 in occlusal view. A, P₃. B-B', M¹. C-C', M². D-D', M³⁻⁴. B-D stereopairs. Scale = 1mm.

that the crown is somewhat twisted. In *B. parvus* P₂ is larger and relatively longer, with a crown that extends further beyond the roots, particularly anteriorly, giving the anterior end of the tooth a shelf-like appearance in lateral view. The crest is less clearly defined than in *B. brutyi* and approximately parallel to the axis of the I₂-P₂ interval.

The crown of P_2 shows less lingual-buccal asymmetry than in *B. brutyi*. The posterior end of the crown rises higher and more steeply than in *B. brutyi* with a distinct hump above the posterior root of the tooth, posterior to which the crown increases only slightly in height. The P_2 of *B. triradiatus* is similar to, but larger than, that of *B. brutyi*. It is wider but shorter than P_2 in *B. parvus* and almost circular in dorsal view. Although it protrudes beyond the roots in all directions, it is flatter than in *B. brutyi* and *B. parvus*. As with *B. brutyi*, the buccal side is displaced ahead of the lingual side and as with *B. parvus*, in lateral view the crown has an anterior 'lip'. The anteroposterior crest is poorly developed. A P_2 (NMV P180016) assigned to *B. triradiatus* by Turnbull et al. (1987) is considerably larger than and different to P_2 in the Holotype. It is 1-rooted, in contrast to P_2 in the Holotype, which has 2 or 3 roots. NMV P180016 could possibly be a *B. triradiatus* P_2 . P_2 is not known from *B. wakefieldi* but appears to have been 1-rooted.

The plagiaulacoid crown of P_3 is longer and taller in *B. brutyi* than *B. wakefieldi*, larger in *B. parvus* and larger again in *B. triradiatus*. P_3 of *B. brutyi* has 5 or 6 dorsal cusps and associated ridges. The anterior edge of P_3 rises vertically in *B. brutyi*, curving back dorsally to an almost horizontal serrated crest. The anterior profile is straight in *B. wakefieldi*, but leans backwards slightly as it rises to an also horizontal crest. The anterior root descends from the crown more anteriorly and buccally in *B. wakefieldi* than in *B. brutyi*. In *B. triradiatus* and *B. parvus*, the anterior profile of P_3 curves forward then backward as it rises, giving the corrugated tooth a 'fanned' appearance and increasing the length of the dorsal edge. In *B. triradiatus* the anterior root curves forward slightly as it rises, with its convex profile continued by the crown. In *B. parvus* the root rises vertically to the base of the crown, then the crown expands gently forward. The P_3 blade is slightly concave lingually and convex buccally. The exposed portion of the anterior root of P_3 protrudes further beyond the jaw margin buccally in *B. brutyi* than in *B. parvus*. It is also in high relief in *B. wakefieldi* and *B. triradiatus*. In *B. parvus*, the posterior end of the crest has shifted lingually and backwards (relative to its position in *B. brutyi*). Thus the anterior angle between the long axis of the P_3 crest and the molar row is greater in *B. parvus* than *B. brutyi*, as is the angle between this crest and its underlying roots. The posterior root of P_3 is also smaller buccally in *B. parvus* than in *B. brutyi* and is smaller again in *B. wakefieldi*

because the posterior end of the crest and hence the direction of the bite force in that region has shifted lingually. The anterior end of P_3 is more attenuated in *B. parvus* than in the other species. Some specimens of *B. brutyi* have cracks running from the dorsal cutting edge basally and backwards, stopping near the base of the crown. P_3 s of each of the other species have similar cracks. They are particularly frequent and extensive in *B. triradiatus*. The P_3 s of *B. triradiatus* also generally show more wear on the anterior end of the dorsal cutting edge than is evident in the other species.

Lower molars are bunodont in *Burramys*. They differ mainly in size, M_1 cusp morphology and degree of reduction of M_4 . Some unworn molars of *B. brutyi* are slightly crenulate, unlike other species of *Burramys*, but since crenulation is rare in *B. brutyi* and since molars of the other fossil species are poorly known, this feature is not regarded as diagnostic. The molar gradient is greater in *B. parvus* than in other species.

M_1 is approximately the same size in *B. brutyi* and *B. wakefieldi* and is larger in *B. parvus*. It has two roots in each of these species. M_1 is not known from *B. triradiatus* but judging from its alveoli was 3-rooted and relatively small, with $M_4 < M_1 < M_3 < M_2$. The trigonid rises more steeply against P_3 in *B. brutyi* and *B. wakefieldi* than in *B. parvus*, with the protoconid taller in comparison to the metaconid. P_3 and M_1 are therefore more disparate in height in *B. parvus* than in *B. brutyi* or *B. wakefieldi*. Posteriorly, the crown extends further beyond the roots in *B. parvus* than in the other species. In *B. wakefieldi* the entoconid is particularly tall. In all species, the M_1 postmetacristid is continuous with the longitudinal axis of the dorsal crest of P_3 . In *B. brutyi* and *B. parvus* the premetacristid swings buccally to meet the postmetacristid, creating a disjunction between the P_3 crest and the lingual crests of M_1 . The postprotocristid/premetacristid angle is more obtuse at the metaconid in *B. brutyi* than *B. parvus* because the metaconid is more posteriorly positioned in the former than the latter. The break in the P_3 - M_1 blade system is therefore, longer in *B. brutyi* than in *B. parvus*. In *B. wakefieldi* the protoconid is more lingually positioned so that the crests associated with the P_3 and M_1 protoconid, metaconid and entoconid form an almost straight line.

M_2 is smaller in *B. brutyi* than *B. triradiatus* or *B. parvus*. M_2 of the latter is slightly longer and narrower than that of *B. triradiatus*. It is proportionately shorter in *B. brutyi* than *B. parvus* and

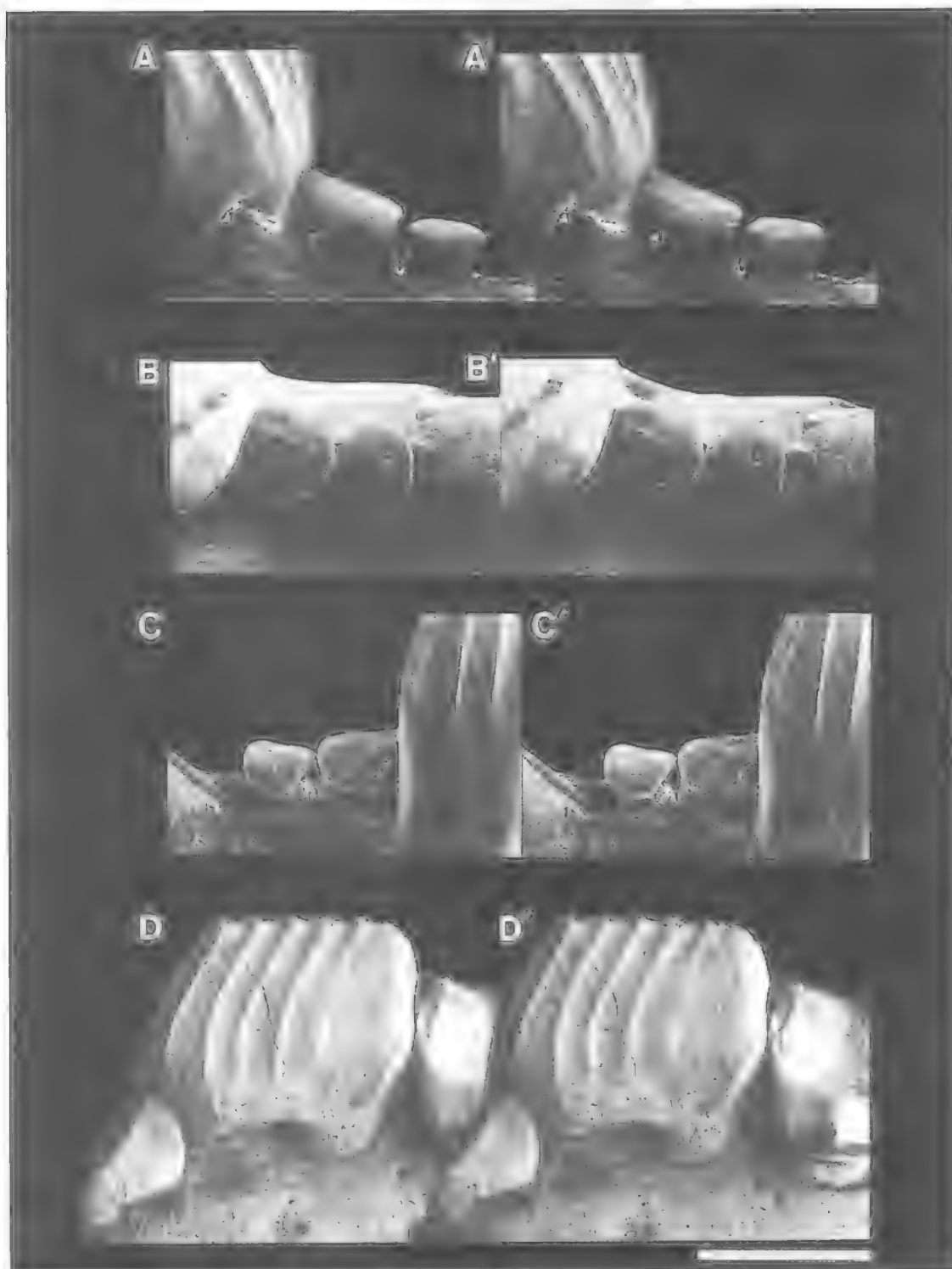


FIG. 9. *B. brutyi* sp. nov. A-C, left P₁₋₂ with I₂ alveolus and anterobasal portion of P₃, holotype QMF30102 in (A-A') lingual, (B-B') occlusal and (C-C') buccal views. D-D', left P₂₋₃ and anterior portion of M¹, paratype QMF30091 in lingual view. A-D stereopairs. Scale = 1 mm.

TABLE 4. Measurements of *B. brutyi* types. From holotype where possible. M₃₋₄ lengths and widths, M₁₋₃ and M₁₋₄ from paratype QMF30176. All upper tooth measurements from paratype QMF30176. Abbreviations as for Table 1.

Lower teeth		Upper teeth	
P ₁ L	0.48	P ² L	1.01
P ₁ MW	0.55	P ² MW	0.60
P ₂ L	0.62	P ³ L	1.91
P ₂ MW	0.64	P ³ AW	0.92
P ₃ L	1.76	P ³ PW	1.21
P ₃ AW	1.07	P ³ MW	1.21
P ₃ PW	1.23	P ³ LH	1.56
P ₃ MW	1.31	P ³ BH	1.64
P ₃ LH	1.45	M ¹ L	1.11
P ₃ BH	1.76	M ¹ AW	1.17
M ₁ L	1.21	M ¹ PW	1.21
M ₁ AW	0.83	M ¹ MW	1.39
M ₁ PW	0.97	M ² L	0.96
M ₂ L	1.10	M ² AW	1.13
M ₂ AW	0.88	M ² PW	0.89
M ₂ PW	0.94	M ³ L	0.82
M ₃ L	0.98	M ³ AW	0.90
M ₃ AW	0.85	M ³ PW	0.66
M ₃ PW	0.80	M ⁴ L	0.64
M ₄ L	0.66	M ⁴ AW	0.67
M ₄ AW	0.64	M ⁴ PW	0.40
M ₄ PW	0.50	M ¹⁻²	2.07
M ₁₋₂	2.30	M ¹⁻³	2.90
M ₁₋₃	3.18	M ¹⁻⁴	3.51
M ₁₋₄	3.83		

very slightly shorter than *B. triradiatus*. M₂ is not known for *B. wakefieldi*. It has two roots in each species except for *B. triradiatus*, in which it has three. In a few (<5%) of *B. brutyi* specimens the anterior alveolus has, ventrally, a septum (or remainder thereof) subdividing it basally into 2 compartments, suggesting a root bifurcated at its tip. This condition may be intermediate between the 2- and 3-rooted conditions. In *B. brutyi* and *B. parvus* there is frequently a small cuspid halfway along the lingual margin of the crown, at the junction of the postmetacristid and the preentocristid. Sometimes the cuspid is not clearly differentiated from the postprotocristid. It is the same size in both species even though the tooth is larger in *B. parvus*. The cuspid is not evident in *B. triradiatus*, although there is a small dorsal protuberance on the anterior end of the preentocristid of NMV P158628. In each species the postprotocristid curves lingually from the protoconid before straightening and running approximately parallel to the tooth axis until interrupted by the transverse hypoconid-entoconid lophid. Postprotocristid curvature is less extreme in *B.*

brutyi than the other species. The cristid obliqua lies parallel to the tooth axis, forming a posterobuccal cingular pocket between itself and the postprotocristid. In all species the buccal cusps are bulbous. The hypoconid causes the posterobuccal corner of the tooth to extend beyond its basically rectangular outline. The lingual cusps are slightly ahead of the buccal cusps, skewing the sides of the tooth slightly. They are more crescentic than the buccal cusps and, together with their associated crests, form a blade-like structure.

M₃ is similar to, but smaller than, M₂. Cusps are lower and basins shallower, with the crown surface showing more wear than M₂. M₃ is smaller in *B. brutyi* than the other species, is slightly larger in *B. triradiatus* than *B. parvus* and is not known from *B. wakefieldi*. Interspecific comparisons of M₃ are as for M₂ except that in *B. brutyi* and *B. parvus*, but not *B. triradiatus*, the lingual-buccal skew is slightly more pronounced than in M₂. In all species M₃ is slightly shorter anteroposteriorly than M₂. In *B. triradiatus* the protoconid and hypoconid of M₃ are subequal whereas in M₂ the hypoconid is larger. In M₃ there is a distinct cleft dividing the rounded protoconid and hypoconid.

M₄ in *B. brutyi* and *B. wakefieldi* has 2 roots, whereas in *B. triradiatus* it has 3 and in *B. parvus* 1. While most specimens of *B. brutyi* have 2 roots or alveoli for M₄, some have 3 and a few had 1 root. Such variation is not evident in the *B. triradiatus* or *B. parvus*. M₄ is not known for *B. wakefieldi* or *B. triradiatus* but the alveoli of *B. triradiatus* suggest that it was far less reduced than in *B. parvus* and possibly less reduced than in *B. brutyi*. M₄ is low-crowned, with low cusps which quickly wear down. It is smallest and most degenerate in *B. parvus*.

Upper teeth of *Burramys* anterior to P² have not been recognised from Riversleigh or Hamilton, so discussion of the upper dentition will be limited to P²⁻³ and M¹⁻⁴. Skull fragments and upper teeth of *B. wakefieldi* are unknown. The upper dentition of *B. triradiatus* is known only from isolated teeth.

Maxilla. Palatal vacuities are smaller in *B. brutyi* than *B. parvus*. The anteroventral opening of the infraorbital foramen is also smaller (and less round) in *B. brutyi*, as are foramina in the alisphenoid and squamosal. Known bones of the skull are more robust in *B. brutyi* than in *B. parvus*. In both species the maxilla is swollen around the P³ alveolus, between the lachrymal

and the infraorbital foramen. This swelling is more extensive in *B. parvus* than *B. brutyi*, with P^3 and the anterior limit of the molar row beginning further forward in the living species. In ventral view, the anteromedial limit of the zygomatic arch in *B. brutyi* is level with a point midway between the protocone and protoconule of M^1 . In *B. parvus* it is midway between the metaconule and protocone of M^1 . The upper molar gradient is steeper in *B. parvus* than in the other species. In *B. brutyi* the molar row rotates buccally around the maxilla from front to back, to a greater degree than occurs in *B. parvus*.

Upper dentition. P^2 of *B. brutyi* is 2-rooted and similar to, although slightly larger than, P_2 . A weak crest runs from a small cuspule at the highest point on the crown, which is midway along the raised posterior edge, to the anterior base of the crown. Lingually and buccally the crown slopes towards the roots. The base of the crown expands lingually over the posterior root, extending the crown outline posterolingually. This swelling is less pronounced in *B. parvus*. In crown view the tooth is teardrop-shaped, being just wider than the transverse diameter of the anterior root. In *B. parvus*, by contrast, the 2-rooted P^2 crown expands beyond the roots for its whole length (more so posteriorly than anteriorly). In both species the crown is parallel to the edge of the medially inclined palate, forming an angle with P^3 and the molar row. Although P^2 for *B. triradiatus* has not been identified, the small, single-rooted tooth (NMV P180016), determined by Turnbull et al. (1987) to be a P_2 , is similar to P^2 s of *B. brutyi* and *B. parvus* and is interpreted here to be P^2 .

In *B. brutyi*, as in *B. triradiatus* and *B. parvus*, P^3 is similar to P_3 . Regarding P^3 anteroposterior length, *B. brutyi* < *B. parvus* < *B. triradiatus*. P^3 is dorsoventrally shortest in *B. brutyi* and slightly taller in *B. triradiatus* than *B. parvus*. It is similarly shaped in all three species but in *B. brutyi* the crown decreases in anteroposterior length from base to occlusal edge, whereas in *B. parvus* and *B. triradiatus* the ventral edge of the blade is at least as long as base of the crown. In anterior view, P^3 of *B. brutyi* is as wide as that of *B. parvus* at its base, but tapers more rapidly and is hence thicker at the occlusal edge and more robust in appearance. In *B. triradiatus* the tooth is thicker basally than in *B. parvus* because of a broader cingulum (see below). It is thicker for most of its height but tapers to almost as thin an edge as does *B. parvus* P^3 . Whereas the dentary turns medially

immediately anterior to P_3 , the maxilla of *Burramys* turns medially only anterior to P^2 . P^3 therefore does not appear to turn out from the molar row as much as P_3 ; its crest is approximately parallel to the molar row. Consequently it does not have to retract anterobasally (as with P_3) to insert into the bone and unlike P_3 its anterior edge, seen in lateral view, may appear to extend slightly forward basally. Probably as a consequence of this, the buccal-convexity/lingual-concavity is, in all species, less pronounced than in P_3 . In occlusal view, P^3 of *B. brutyi* is basically rectangular, but with the anterior end curving to a rounded point and the posterior corners rounded. In *B. parvus* and *B. triradiatus* it is more ovoid, the anterior end again being a little narrower than the posterior end, and pointed. There is a narrow cingulum, poorly developed at the anterior end, along the lingual and buccal sides of the crown. The cingulum is very weak in *B. brutyi*, slightly better developed in *B. parvus* and significantly better developed in *B. triradiatus*. In this species the cingulum is sometimes emphasised lingually by a vertical wear facet that terminates abruptly at the cingulum. In *B. triradiatus* and to some extent in *B. parvus* the second and sometimes third lingual ridges merge into the first which forms a curb that arcs back toward the cingulum. This curb is less prominent in *B. brutyi*, in which ridges approach the cingulum without merging.

In all species M^1 has 3 roots — a larger lingual and 2 smaller buccal roots. In *B. brutyi* M^1 is wider than it is long. In *B. parvus* and *B. triradiatus* it is about as wide as long. In all 3 species there is a swelling anterobuccal to the paracone such that the anterobuccal corner of the tooth is a little larger than the posterobuccal corner. In *B. brutyi* there is a distinct buccal cingular basin or shelf at the intersection of the post-paracrista and the premetacrista extending back to the level of the metacone and forward nearly as far as the paracone. It is sometimes delimited anteriorly by a small crest running buccally from the paracone. In *B. parvus* this pocket is little more than a sloping cingular shelf. In *B. triradiatus* it is a narrow cingulum following the rounded paracone and metacone buccally (Turnbull et al., 1987, fig. 5A). The ectoloph of *B. brutyi* is roughly parallel to the anteroposterior axis of the tooth. As with *B. parvus*, the paracone is significantly larger than the other cusps, retaining its height as the tooth wears. The protoconule and metaconule are less developed in *B. brutyi* and *B. triradiatus* than in *B. parvus*. Hence in

occlusal view, M^1 of *B. brutyi* is basically rectangular, with the anterior and posterior ends of the tooth parallel. In *B. parvus* it is longer and more curved lingually than buccally because of the inflated protocone and metacone. In occlusal view there is an indentation between the paracone and metacone in *B. brutyi* and *B. triradiatus*, whereas in *B. parvus* the crown outline between those cusps is almost straight.

M^2 is rectangular in *B. brutyi* (shorter anteroposteriorly) and considerably smaller than in either *B. triradiatus* or *B. parvus*, in both of which it is about as wide as it is long. In all species it has 3 roots and a small cingular pocket anterobuccal to the paracone, bounded lingually by a short preparacrista that runs perpendicularly from the anterior edge of the tooth to the paracone. The buccal cusps and their associated crests are blade-like in comparison to the more rounded lingual cusps. In *B. triradiatus* the buccal cusps are more pointed and the lingual cusps more rounded than in *B. brutyi* or *B. parvus*. The transverse lophs are also taller and consequently the cingular and central basins deeper. The protocone and metacone are more approximated than in other species, as are the paracone and metacone. In unworn specimens of *B. parvus* the relative cusp heights are as reported for *B. triradiatus* (Turnbull et al. 1987): protocone exceeds metacone while paracone is subequal to the metacone. In worn M^2 s of *B. parvus* the lingual cusps are lower so that the paracone exceeds the metacone which exceeds the protocone which is subequal to the metacone. This pattern of cusp wear appears to be the same in *B. brutyi*.

M^3 of *B. brutyi* is similar to M^2 but is smaller, proportionately a little narrower (because the lingual cusps are less bulbous) and with cusps a little lower. The posterior cusps are more reduced than the anterior cusps and the metacone, in particular, is relatively lower. The metacone is slightly further forward than in M^2 so that the posterolingual corner of the tooth is more rounded in occlusal view. This feature is similar to the condition in *B. triradiatus* and, even more so, to the condition in *B. parvus*. The transverse lophs, pre- and post-cingula and their associated basins soon wear down to the level of the central basin. M^3 is most reduced posteriorly in *B. parvus* and least reduced in *B. triradiatus*.

M^4 is larger, both relative to other molars and absolutely, in *B. brutyi* than in *B. parvus* and is also less posteriorly reduced. The posterior cusps, especially the metacone, are markedly reduced. The anterior cusps, although low and rapidly

worn, are distinct in unworn teeth and remain distinguishable until late wear stages. Although the cusps, their associated crests and basins are low and quickly levelled, worn M^4 s of *B. brutyi* shows more surface morphology than those of *B. parvus*, in which even newly-erupted M^4 s are almost featureless. M^4 has 3 roots in *B. brutyi*. Ride (1956) reports a double-rooted M^4 in *B. parvus* but it appears from the specimens examined that the basic condition in *B. parvus* is a 3-rooted M^4 , perhaps with a reduced number of roots in some specimens.

INTRAGENERIC PHYLOGENETIC ANALYSIS

Thirty-five characters were investigated for their potential to contribute to an analysis of the relationships between species of *Burramys*. *Cercartetus nanus*, *C. lepidus*, *C. caudatus* and *C. concinnus* were used as the primary outgroup since *Burramys* and *Cercartetus* are sister groups (Archer, 1984; Aplin & Archer, 1987). *Trichosurus caninus*, *T. arnhemensis*, *T. vulpecula*, *Spilocuscus maculatus* and *Phalanger carmelitae* were used as a secondary outgroup because DNA hybridisation indicates that burramyids and phalangerids are sister groups (Springer & Kirsch, 1989). Character numbers refer to Table 5; unnumbered characters are not included in the analysis.

1. Body size. Jaw lengths suggest that *B. brutyi* and *B. wakefieldi* were of similar body size. *B. triradiatus* and *B. parvus* are larger and approximately the same size as each other. *Cercartetus lepidus*, the smallest of its genus, is also regarded as the most primitive (Archer, 1984). Phalangerids are larger than burramyids but this is likely to be a derived condition; diverse taxa exhibit a general tendency for increasing body size over time (Maurer et al., 1992). The small size of *C. lepidus* suggests that larger size is apomorphic within *Burramys*. In our discussion of character states, a morphological feature is regarded as large only if its greater size is independent of increased body size.

2. Robustness. The dentary and maxilla of *B. parvus* are more slender than those of other *Burramys*, despite being larger. All species of *Cercartetus* have similarly slender jaws. *Trichosurus*, *Spilocuscus* and *Phalanger* are more robust than *Cercartetus* or *B. parvus*, but being several times larger than burramyids, they do not form a useful comparison in this regard. The slenderness of *Cercartetus* suggests that increased robustness is apomorphic in burramyids.

3. Length of I_2 - P_2 interval. The interval occupied by I_2 , P_1 and P_2 is longer relative to jaw length in *B. parvus*

TABLE 5. Characters and character polarities for intrageneric phylogenetic analysis of *Burramys* species. Plesiomorphic state denoted by 0; ? indicates that information on character is unavailable. A and B indicate alternative derived states.

Character	<i>B. brutyi</i>	<i>B. wakefieldi</i>	<i>B. triradiatus</i>	<i>B. parvus</i>
1 Body size	0	0	1	1
2 Robusticity	1	1	1	0
3 Length of I ₂ -P ₂ interval	1	1	2	0
4 Length of I ₁	0	?	2	1
5 Basal thickening of I ₁	1	?	1	0
6 Number of roots P ₁₋₂	0	1A	1B	0
7 Arrangement of alveoli P ₁₋₂	1	?	?	0
8 Size of P ₃	1	1	2	1
9 Size disparity between P ₃ roots	1	3	2	2
10 Number of ridges P ₃	1	1	3	2
11 Curvature of P ₃ anterior profile	0	0	1	1
12 Concave/convex P ₃	0	0	1	1
13 Arched dorsal edge P ₃	0	0	1	2
14 Divergence of P ₃ from molar row	1	3	2	2
15 Transverse compression P ₃	1	1	3	2
16 Distinct M ₁ talonid and trigonid	1	0	?	1
17 M ₁ protoconid position	0	1	?	0
18 M ₁ metaconid position	0	0	?	1
19 Relative length lower molars	2	2	1	0
20 Neomorphic cuspid	1	?	0	1
21 Loph(id) development M ₂₋₃ , M ₂₋₃	1	?	0	1
22 No. roots M ₁₋₃	0	0	1	0
23 No. roots M ₄	0	0	1A	1B
24 Reduction of M ₄	1	1	0	2
25 Size of maxillary vacuities	0	?	?	1
26 Anterior limit P ₃	1	?	?	0
27 Rotation of upper molar row	1	?	?	0
28 Inflation of lingual cusps M ¹	0	?	0	1
29 Lingual displacement of M ¹ paracone	0	?	0	1

than in *B. brutyi* or *B. triradiatus*, with *B. triradiatus* the shortest. This region is incomplete in the holotype of *B. wakefieldi* but appears to be about the same length as in *B. brutyi*. This interval is relatively long in *Cercartetus* and phalangerids, indicating that this is the plesiomorphic state.

4. I₁ length. I₁ is longer in *B. parvus* than *B. brutyi* and longer again in *B. triradiatus* (unknown in *B. wakefieldi*). It is shorter in *Cercartetus* than *Burramys* and is shorter in phalangerids. A long I₁ is regarded as apomorphic.

5. Thickened base of I₁. In *B. brutyi* and *B. triradiatus* I₁ is thick basally (thicker in *B. triradiatus*) and immediately begins to taper; approximately half way along the exposed portion of the tooth it thins markedly then attenuates to the tip. In *B. parvus* I₁ tapers gradually without marked reduction at a particular point. In *Cercartetus*, *Trichosurus*, *Spilocuscus* and *Phalanger* I₁ does not change suddenly in diameter, suggesting that a basally thickened I₁ is apomorphic.

Shape of P₁. P₁ is not known for *B. wakefieldi* or *B.*

triradiatus. In *B. brutyi* it is small, rounded and similar to P₂. In *B. parvus* P₁ is intermediate between the cap-like P₂ and the slightly elongate, procumbent I₂. In *C. caudatus* and *C. lepidus* P₁ and P₂ are both button-like and upright; in *C. nanus* and *C. concinnus* P₁ resembles I₂ almost as much as P₂. *Trichosurus* and *Phalanger* species have extensive diastemata, lacking P₁ and P₂ analogous to those of burramyids. It is therefore unclear which state of P₁ is more plesiomorphic and although this character may be phylogenetically significant, a satisfactory polarity assignment cannot be made.

6. Number of roots P₁ and P₂. *Burramys brutyi* and *B. parvus* have double-rooted P₁ and P₂. *Burramys triradiatus* has a triple-rooted P₂ and double- or triple-rooted P₁; the number of roots is not clear due to damage in the available material. P₁ and P₂ each appear to have been single-rooted in *B. wakefieldi*. P₁-P₂ of *Cercartetus* possess sometimes one and sometimes two roots. P₁-P₂ of *Trichosurus* and *Phalanger* are either extremely reduced or absent. Outgroup analysis does not resolve the polarity of this character. The normal marsupial premolar condition is two-rooted so this is

taken to be the plesiomorphic condition. *Burramys wakefieldi* and *B. triradiatus* are interpreted as having alternative derived states.

7. Arrangement of P₁₋₂ alveoli. In *B. parvus* the alveoli of P₁₋₂ are in a straight line between I₂ and P₃. In *B. brutyi* the anterior alveolus of P₂ is lingual to its posterior alveolus and the posterior alveolus of P₁ is lingual to its anterior alveolus. *B. wakefieldi* and *B. triradiatus* have different numbers of roots for P₁₋₂ from *B. brutyi* and *B. parvus*, so their alveoli are not all homologous. In all species of *Cercartetus* the alveoli of P₁₋₂ lie in a straight line; this is also the case for *Trichosurus*, *Spilocuscus* and *Phalanger* (where the teeth occur). Linearly-arranged alveoli are therefore thought to be plesiomorphic for burramyids.

8. Size of plagiaulacoid premolar. The sectorial premolar of *Cercartetus* and phalangerids (and M₁ of *C. concinnus*) is smaller than that of *Burramys*. It is therefore assumed that an enlarged plagiaulacoid premolar is synapomorphic for *Burramys* and apomorphic within the genus. Although P₃ of *B. parvus* is larger than that of *B. wakefieldi* or *B. brutyi*, log-scaled plots of P₃ buccal crown surface area against jaw length (unpubl. data) suggest that P₃ of *B. parvus* is not disproportionately large for its body size. P₃ of *B. triradiatus*, on the other hand, departs significantly from the line of best fit for P₃ size against body size, being disproportionately large. P₃ of *B. wakefieldi* falls below the line, suggesting that it is disproportionately small, but Studentized residuals do not show its departure from the line to be significant.

9. Relative sizes of anterior and posterior roots of plagiaulacoid premolar. Buccally, the posterior root of P₃ is smaller, relative to its anterior root and crown, in *B. wakefieldi* than in other *Burramys*. The posterior root of P₃ is smaller (relative to the anterior root and the crown) in *B. parvus* than in *B. brutyi*. The anterior root of the large P₃ of *B. triradiatus* is massive; although the posterior root is comparatively small, the disparity is not as great as that in *B. wakefieldi*. In *Cercartetus* and phalangerids, the anterior and posterior roots of the sectorial premolar are subequal; this is thought to be the plesiomorphic condition.

10. Number of ridges on plagiaulacoid premolar. In *B. brutyi* and *B. wakefieldi* there are 5 or 6 ridges on each of the buccal and lingual faces of P₃ and 5 or 6 associated dorsal cusps. The lack of posterior and weakness of anterior cusps in the holotype of *B. wakefieldi* appears to be the result of extreme wear on the formerly serrated tooth. In *B. parvus* there are commonly 7 ridges and cusps and in *B. triradiatus*, 9. Phalangerids with smaller, unridged P₃s are thought to be more plesiomorphic than those with larger, ridged P₃s (Flannery et al., 1987); all have fewer ridges and cusps than *Burramys*. *Cercartetus nanus* and *C. caudatus* have a single sharp dorsal cusp on the sectorial premolar and *C. concinnus* one main cusp on its premolariform M₁. A larger number of ridges and

cusps is regarded as more derived within *Burramys* and a synapomorphy of the genus.

11. Curvature of anterior profile of P₃. In lateral view, P₃ of *B. wakefieldi* and *B. brutyi* has a relatively straight (approximately vertical) anterior profile. In *B. triradiatus* and *B. parvus* the crown expands anteriorly to produce a curved profile. The sectorial P₃ of *Cercartetus* does not curve forward anteriorly (although the autapomorphic premolariform M₁ of *C. concinnus* does). Anterior curvature may be associated with increased P₃ size, with enlargement having been achieved by anterior extension of the crown. However P₃s of *T. caninus* and *T. vulpecula*, which are curved, are smaller than those of *Spilocuscus* and *Phalanger*, which are less curved. Size and curvature are therefore not necessarily linked. It is possible that Miocene P₃s represent primary enlargement of the tooth without the functional elaboration of other species, in which the inflated anterior edge may disperse stress, increase occlusal area, or perform some other function. A curved anterior profile is regarded as apomorphic within Burramyidae.

12. Lingual concavity/buccal convexity of P₃. The P₃ blade of *Burramys* is concave lingually and convex buccally (particularly anteriorly). The contrast between lingual and buccal curvature is least pronounced in *B. wakefieldi* and *B. brutyi* and more pronounced in *B. parvus* and slightly more in *B. triradiatus*. As with anterior profile curvature, this feature occurs in *Trichosurus* but not in *Cercartetus*, *Spilocuscus* or *Phalanger*. It is regarded as apomorphic.

13. Arching of dorsal edge of P₃. The dorsal edge of P₃ is arched in *B. parvus*; in the other species it is straight, but in *B. triradiatus* there is a slight curvature at the anterior end of the blade. The sectorial teeth of *Cercartetus* do not have a dorsal blade edge homologous with that of *Burramys* and so do not provide a useful comparison. The dorsal edge of P₃ is straight in phalangerids and this is assumed to be the plesiomorphic condition.

14. Divergence of P₃ from anteroposterior axis of molar row. In *Burramys*, the longitudinal axis of P₃ departs from the ramus such that it forms an angle with the anteroposterior molar row axis. This angle is largest in *B. wakefieldi* and is larger in *B. parvus* and *B. triradiatus* than in *B. brutyi*. In *Cercartetus* the longitudinal axis of the lower sectorial tooth is parallel to the anteroposterior axis of the molar row and within phalangerines, a more oblique placement of P₃ is regarded as apomorphic (Flannery et al., 1987). Divergence of P₃ from the anteroposterior axis of the molar row is a synapomorphy of *Burramys*; within *Burramys*, the plesiomorphic condition is taken to be a less divergent P₃.

15. Transverse apical compression of P₃. In anterior view, the crown of P₃ of *Burramys* tapers from the base, attenuating dorsally then terminating apically

with a serrated longitudinal median ridge. This transverse apical compression is least pronounced in the Miocene species and most pronounced in *B. triradiatus*. Crowns of the sectorial premolars of *Cercartetus*, *Trichosurus*, *Spilocuscus* and *Phalanger* are less attenuated than those of *Burramys*. Increased dorsal transverse compression is synapomorphic for *Burramys*. Laterally compressed P3s are regarded as more derived than those with thicker apices.

16. Distinction of talonid and trigonid of M₁. In *B. wakefieldi* the talonid and trigonid of M₁ are clearly demarcated in occlusal view by lingual and buccal indentations. In *B. brutyi* and *B. parvus* the talonid and trigonid are less distinct. M₁ is not known for *B. triradiatus*. Talonids and trigonids are more distinct in *Cercartetus* than in *Burramys*, indicating the plesiomorphic state. The fused talonid and trigonid departs further from primitive tribosphenic morphology. Alternatively, the structure of M₁ in *B. wakefieldi* could be autapomorphic, with the crests defining the talonid and trigonid functioning primarily as buttresses for the anterolingual crests which may, in this animal, have extended the function of P₃. However, the former hypothesis is preferred.

17. Lingual displacement of protoconid of M₁. The protoconid of M₁ is displaced further lingually in *B. wakefieldi* than in *B. brutyi* or *B. parvus* so that in *B. wakefieldi* the crests associated with P₃ and the M₁ protoconid, metaconid and entoconid form an almost straight line. The position of the protoconid is variable in *Cercartetus* and phalangerids. In the primitive tribosphenic molar, the protoconid is a buccal cusp, so lingual displacement is regarded as apomorphic.

18. Anterior displacement of metaconid of M₁. The paraconid is absent in *Burramys* and the most anterior lingual cusp is the metaconid. In *B. parvus* the metaconid is more anterior than in *B. wakefieldi* or *B. brutyi*, narrowing the gap in the P₃-M₁ crest. In the Phalangeridae and *Cercartetus* position of the metaconid relative to the protoconid is variable. Outgroup analysis does not resolve the polarity of this character. The metaconid of *B. parvus* occupies the position that in a plesiomorphic (tribosphenic) molar would have supported the paraconid, so the anteriorly displaced metaconid is regarded as apomorphic.

Inclination of M₁ trigonid against P₃. The trigonid of M₁ rises more steeply against the posterior face of P₃ in *B. brutyi* and *B. wakefieldi* than in *B. parvus*. Neither *Cercartetus* nor phalangerids give a clear indication of the polarity of this character. It has developed a number of times in phalangerids and pilkipildrids and is probably homoplasious.

19. Relative length of lower molars. M₂₋₄ of *Burramys* differ in their lengths (relative to widths) such that *B. brutyi* < *B. triradiatus* < *B. parvus*. M₂₋₄ are not known for *B. wakefieldi* but judging by their alveoli, they were of similar proportions to those of *B. brutyi*. In

Cercartetus, *Trichosurus*, *Spilocuscus* and *Phalanger*, the molars are relatively long, implying that this is the plesiomorphic condition.

20. Neomorphic cuspid at intersection of postmetacristid and preentocristid of M₂₋₃. In *B. brutyi* and *B. parvus* there is usually a small neomorphic cuspid approximately half way along the lingual margin of the crown, at the junction of the postmetacristid and the preentocristid. This cuspid is not present in the few available lower molars of *B. triradiatus*, nor in *Cercartetus*, *Trichosurus*, *Spilocuscus* or *Phalanger*, suggesting that it is apomorphic in the Burramyidae.

Lingual cusps skewed ahead of buccal cusps of M₂₋₃. In *B. triradiatus*, the lingual cusps of M₂₋₃ are ahead of the buccal cusps, skewing the sides of the teeth slightly. This skew is less evident in *B. brutyi* and slightly less again in *B. parvus*. *Cercartetus caudatus* is about as skewed as *B. parvus* and is the least skewed of species of *Cercartetus*, with *C. nanus* and *C. concinnus* showing about the same, increased degree of skew. The amount of skew on the molars is variable within phalangerids, ranging from very minor to quite pronounced. Outgroup analysis gives no clear indication of whether skewed molars are plesiomorphic or derived in *Burramys*.

21. Transverse loph(id)s of M₂₋₃ and M₂₋₃. The transverse lophs and lophids of M₂₋₃ and M₂₋₃ are more complete in *B. triradiatus* than in *B. brutyi* or *B. parvus*, such that the central basins and the pre- and post-cingular basins of the teeth are deeper and more clearly defined in the Hamilton species. *Cercartetus* lacks transverse loph(id)s but this is probably apomorphic for the genus; lophs and lophids are well formed on the molars of the more plesiomorphic phalangerids. *Burramys triradiatus* is thought to be relatively plesiomorphic in possessing more complete molar lophs and lophids.

22. Number of roots M₁₋₃. M₁₋₃ are double-rooted in *B. wakefieldi*, *B. brutyi* and *B. parvus*, but in *B. triradiatus* are 3-rooted. Turnbull et al. (1987) regarded the 3-rooted condition as a plesiomorphic retention. However, *Cercartetus*, phalangerids and virtually all marsupials have 2-rooted molars, making the plesiomorphic retention of 3-rooted lower molars by *B. triradiatus* seem unlikely. The 3-rooted lower molars of *B. triradiatus* are interpreted as autapomorphies.

23. Number of roots M₄. M₄ is single-rooted in *B. parvus*, double-rooted in *B. wakefieldi* and *B. brutyi*, and has 3 roots in *B. triradiatus*. M₄ of *Cercartetus* (where it occurs) and phalangerids has 2 roots. The single-rooted and three-rooted M₄ of *B. parvus* and *B. triradiatus* (respectively) are interpreted as alternative apomorphic states derived from a 2-rooted plesiomorphic condition.

24. Reduction of M₄. M₄ is most reduced in *B. parvus* and least reduced in *B. triradiatus*, with the Miocene

species intermediate. *Cercartetus lepidus* and *C. caudatus* (apparently the most plesiomorphic *Cercartetus*) have M4, though reduced; in *C. nanus* and *C. concinnus* M4 is absent. In *Trichosurus* M4 is subequal to M1-3; in *Spilocuscus* and *Phalanger* (which are generally more derived than *Trichosurus*) it is slightly smaller than the anterior molars. Reduction of the posterior molars occurs frequently and independently. Since primitive members of both outgroups have less reduced M4, and since reduction of the molar row posteriorly is commonly a derived state, more reduced M4s are interpreted as apomorphic. Although M4 reduction correlates with M4 root number in *Burramys*, it is treated as a separate character since, as demonstrated by the relative sizes and number of roots of M1-3 in the different species, there is not necessarily a connection between molar size and number of roots.

25. Enlarged maxillary vacuities. Maxillary vacuities are larger in *B. parvus* than in *B. brutyi*. The vacuities of *Cercartetus* do not resolve this character. Vacuities are less extensive in phalangerids than in *B. parvus*, so a less evacuated palate is regarded as plesiomorphic.

26. Anterior limit of P³ relative to zygomatic arch. P³, and therefore the anterior of the upper molar row, is further forward on the maxilla relative to the jugal portion of the zygomatic arch in *B. parvus* than in *B. brutyi*. In *C. concinnus* and *C. caudatus* the teeth are further forward than in *Burramys*; in *C. nanus* (and possibly also *C. lepidus*) the anterior extent of the teeth is similar to that in *B. parvus*. In *S. maculatus*, *P. cameliteae*, *T. arhemensis* and *T. vulpecula*, the cheekteeth commence further forwards. The polarity of this character is not immediately evident, particularly as there are a variety of states within *Cercartetus*; however the anterior disposition of the teeth in phalangerids would argue for that being the plesiomorphic condition.

Enlarged P³ cingulum. The P³ cingulum is slightly more developed in *B. parvus* than *B. brutyi* and significantly more pronounced in *B. triradiatus*. It possibly developed in conjunction with the enlargement of P³ and the generation of greater bite forces at the P³s, functioning as a stopper for P³ during premolar function (as indicated by posterolingual wear facets that stop abruptly at the cingulum in *B. parvus* and *B. triradiatus*) and also protecting the gums from hard food particles sectioned by the premolars. P³s of *Cercartetus* and phalangerids are not sufficiently similar to those of *Burramys* to have homologous cingulae, so outgroup comparison cannot polarize this character. If the enlarged cingulum is linked to P³ size it is not an independent character.

Anterior attenuation of P³. In dorsal view, P³ is more ovoid and in particular, more attenuated anteriorly, in *B. triradiatus* and in *B. parvus* than in *B. brutyi*. P³ is insufficiently similar in *Cercartetus* and phalangerids to *Burramys* to be useful in determining polarity of this character. Anterior attenuation may be associated with

P³ size and is probably linked to anterior inflation of P³; it is not treated as an independent character.

27. Posterobuccal rotation of molars rotate around maxilla. Upper molar row rotation is greater in *B. brutyi* than in *B. parvus*. The upper molars do not rotate buccally in a posterior direction in *Cercartetus*, but they do in phalangerids examined. Using *Cercartetus* as the primary outgroup and applying the principle of commonality, the rotating molar row of *B. brutyi* would be interpreted as more derived than the dental arcade of *B. parvus*.

Pronounced anterobuccal cingular basin M¹. In *B. brutyi* there is a cingular basin on the anterobuccal corner of M¹; in *B. triradiatus* there appears to be a narrow cingular pocket and in *B. parvus* the pocket is little more than a sloping cingular shelf. Inflation of the anterobuccal corner of M¹ is a synapomorphy for *Burramys*. It seems that the degree of definition of the anterobuccal pocket is inversely related to lingual shift of the paracone. Therefore, it is not treated as a separate character.

28. Inflation of lingual cusps of M¹. No maxillary material is available for *B. wakefieldi*. In each of the other species of *Burramys*, the lingual side of M¹ is enlarged by a protoconule on the lingual margin, anterior to the protocone. Both protoconule and metaconule are more inflated in *B. parvus* than in other species and in association with this, lingual cusps of *B. parvus* lie closer to the lingual edge of the tooth than in the other species. There is no protoconule in *C. lepidus* or *C. caudatus*; it is present (relatively undeveloped) in *C. concinnus* and perhaps in a rudimentary state in *C. nanus*. There is no protoconule in *Trichosurus*, *Strigocuscus* or *Phalanger*. An enlarged protoconule is considered apomorphic.

29. Lingual displacement of paracone of M¹. The M¹ paracone of *B. parvus* is displaced lingually so that the ectoloph is oblique with respect to the anteroposterior axis of the tooth. In *B. brutyi* and *B. triradiatus* the ectoloph is approximately parallel to the tooth axis, with the paracone more buccal. The M¹ paracone is not displaced lingually in *Cercartetus* or phalangerids, indicating that this is the plesiomorphic condition.

A Wagner analysis was performed using both ACCTRAN and DELTRAN algorithms of PAUP (Swafford, 1989). Wagner parsimony allows reversal or convergence to construct trees with the fewest steps. Where reversal or convergence would produce an equally parsimonious solution, ACCTRAN accelerates character transformations, favouring reversal, whereas DELTRAN delays transformations, favouring convergence (Wiley et al., 1991). Characters were ordered and a hypothetical ancestral *Burramys*, having all character states 0, was used to root the analysis.

ACCTRAN (Fig. 10) or DELTRAN optimisa-

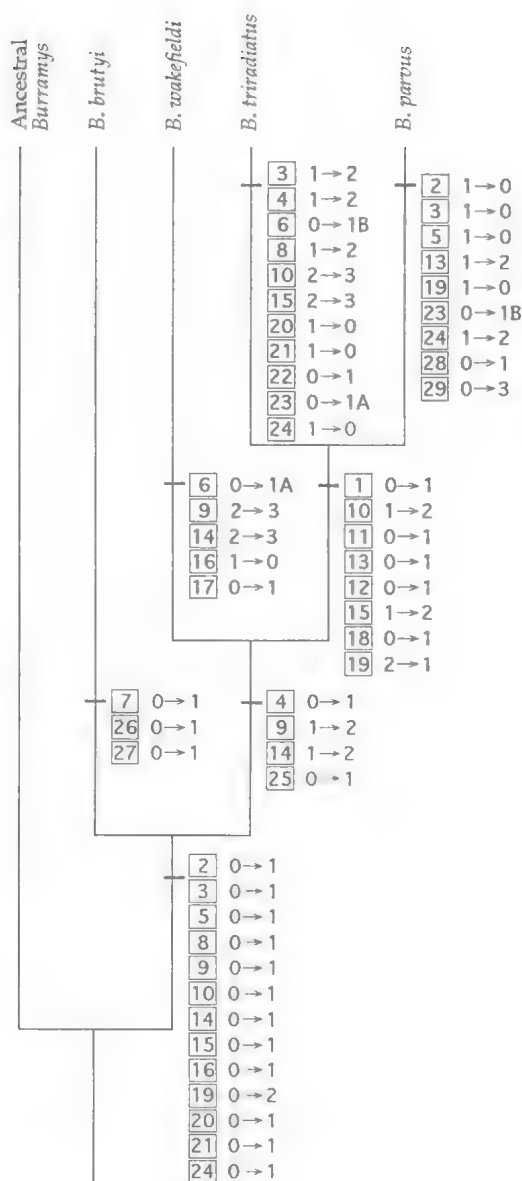


FIG. 10. A phylogenetic hypothesis of intrageneric relationships of *Burramys*. Apomorphies listed at nodes; character numbers in boxes refer to Table 5. Character state transformations indicated by arrows.

tion generated a single most parsimonious tree. The topology of this tree is identical for both algorithms. *Burramys parvus* and *B. triradiatus* form a clade to which *B. wakefieldi* is the plesiomorphic sister group; *B. brutyi* is the plesiomorphic sister group to a clade containing

all other species of *Burramys*. For some characters, the path of transformation differs depending upon whether transformation is accelerated or delayed. There are several convergent character states in the DELTRAN tree, no convergences and more reversals in the ACCTTRAN tree. When transformation is delayed the following character states arise convergently in *B. brutyi* and *B. parvus*: loph(id)s of M₂₋₃ reduce; neomorphic cuspid appears on M₂₋₃; and M₁ talonid and trigonid become less distinct. Basal thickening of I₁ occurs independently in *B. brutyi* and *B. triradiatus*. The relative length of the lower molars decreases independently in *B. brutyi* and *B. wakefieldi*. With delayed transformation *B. parvus* reverses to a more plesiomorphic state of reduced robusticity and relatively long molars, and the relative size of M₄ in *B. triradiatus* increases secondarily. These reversals also occur when transformation is accelerated, as do the following: in *B. parvus* and *B. triradiatus* the relative length of lower molars increases (to a greater degree in *B. parvus*); in *B. parvus* the I₂-P₂ interval increases; in *B. triradiatus* loph(id)s develop on M₂₋₃ and the neomorphic cuspid disappears from M₂₋₃; and in *B. wakefieldi* the talonid and trigonid of M₁ are relatively distinct from one another.

Although a single most parsimonious tree was generated by this analysis, another tree only one step longer placed *B. wakefieldi* as the plesiomorphic sister-group of the other three species, and *B. brutyi* as the plesiomorphic sister-group of the *B. triradiatus* + *B. parvus* clade. A bootstrap analysis using a branch and bound search with 100 repetitions, to place confidence estimates on clades (from ACCTTRAN) found the node defining the *B. triradiatus* + *B. parvus* clade to be supported 84% of the time, but the node separating *B. brutyi* and *B. wakefieldi* occurred in less than 50% of repetitions. Using DELTRAN the *B. triradiatus* + *B. parvus* clade was supported 78% of the time, and the node separating the other 3 species from *B. brutyi* was supported by 55% of repetitions. In both cases, the node separating *B. brutyi* and *B. wakefieldi* is poorly resolved.

DISCUSSION

Burramys brutyi is the only species of *Burramys* at Riversleigh and is not known elsewhere. It is represented by >150 specimens from 23 Sites in Systems A, B and C; it is one of the most widely distributed (spatially and temporally) marsupials at Riversleigh. Its earliest oc-

currence at late Oligocene (Myers & Archer, 1997) White Hunter Site is of similar age to the type locality of *B. wakefieldi* on Mammelon Hill, Lake Palankarina, South Australia (Woodburne et al., 1993).

Metric analyses did not reveal any significant size variation between sites; variation within sites being as great as between sites. This persistence in unchanged form from the late Oligocene through much of the Miocene suggests an unusual degree of ecological stasis for the species.

Fossil *Burramys* in Victoria, South Australia and NW Queensland shows that small existing populations of *B. parvus* are remnants of a previously more diverse and far more widespread lineage, now apparently in decline. This fact urges particular conservation concern for the extant species. Although populations of *B. parvus* are apparently stable, they are threatened both by habitat disturbance and greenhouse warming, which could jeopardise their ability to survive (Geiser & Broome 1993).

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TWO NEW BALBARINE KANGAROOS AND LOWER MOLAR EVOLUTION WITHIN THE SUBFAMILY

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Lower Jaws and teeth of *Nambaroo couperi* sp. nov. and *Wururoo dayamayi* gen. et sp. nov., fossil balbarine kangaroos from the late Oligocene White Hunter Site of Riversleigh, are described. M₁ trigonid cuspid homology in Hypsiprymnodon is re-interpreted such that a reduced protoconid is recognised, the anterobuccal cuspid is regarded as the protostylid and the anterolingual cuspid as the metaconid. The evolution of lophodont lower molars within Balbarinae is examined on the bases of this interpretation and information supplied by the new species. □ Riversleigh, kangaroo, Balbarinae, Nambaroo, Wururoo, cuspid homology, lophodonty.

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The Balbarinae Flannery, et al., 1982 was erected for a group of fossil macropodids in which the M₁ protolophid is markedly compressed. It assumed phylogenetic significance when Flannery (1989) proposed that balbarines were ancestral to both sthenurines and macropodines.

Balbarines form a major component of the fossil kangaroo fauna of Riversleigh and appear to have had a wide distribution in the Oligocene-Miocene of Australia. Three genera and 8 species have so far been named, but it is more diverse than this. *Balbaroo camfieldensis* Flannery et al., 1982 is known from Bullock Creek and *Balbaroo* sp. Flannery et al. (1982) from the Kangaroo Well Local Fauna, both in the Northern Territory. Three species of *Nambaroo* Flannery & Rich, 1986 were described from the Tarkarooloo Local Fauna of South Australia. Unnamed balbarines have been reported by Flannery (1989) from the Kutjumarpu Local Fauna of South Australia and Woodburne et al. (1993) from the Etadunna Formation of South Australia. Riversleigh balbarines include *Balbaroo gregoriensis* Flannery et al., 1982 and 3 species of *Ganawamaya* Cooke, 1992. The present paper includes descriptions based on lower jaws and teeth of a new species of *Nambaroo* and a new genus and species of balbarine.

outlined by Szalay (1969), following Ride (1993). Terminology follows Van Valen (1966), Szalay (1969) and Butler (1990). However, the 'anterior cingulid' is restricted in use to that component of the macropodoid lower molar anterior cingular shelf lying lingual to the anteriorly directed paracristid. 'Precingulid' is refers to that component lying buccal to the paracristid. Van Valen (1966, 1994) used 'precingulid' for the anterior cingular shelf anterobuccal to the paracristid of plesiomorphic mammalian lower molars. The distinction is made here because lingual and buccal components of the macropodoid anterior cingular shelf are demonstrably of different origins. The buccal component is the more plesiomorphic since it occurs in plesiomorphic balbarines such as *Nambaroo couperi* sp. nov. More derived balbarines such as *Wururoo* gen. nov. and *Balbaroo* demonstrate the development of the neomorphic lingual component via lingual displacement of the paraconid and lingual extension of the paracristid. Suprageneric classification follows Aplin & Archer (1987). QMF denotes Queensland Museum fossil collection catalogue numbers. Measurements are in millimetres.

METHODS

Molar homology follows Luckett (1993). Premolar homology follows Flower (1867). Homology of molar structures has been determined by reference to a generalised tribosphenic pattern,

SYSTEMATICS

Family MACROPODIDAE Gray, 1821
Subfamily BALBARINAE Flannery,
Archer & Plane, 1982
Nambaroo Flannery & Rich, 1986

Nambaroo couperi sp. nov.
(Figs 1, 2, 5A; Table 1)

DIAGNOSIS. *Nambaroo* with a hypoconulid at the posterior, buccal base of the entoconid on M₁ and marked convexities along the lateral margins adjacent to the ends of the interlophid valley on all lower molars except M₄.

MATERIAL. Holotype QMF30401, a partial right dentary consisting of the entire horizontal ramus, most of the angular process and portion of the ascending ramus to the level of the damaged condyle. P₃ and M₁₋₄ are preserved; from White Hunter Site, Hal's Hill, D Site Plateau, which has been correlated (Myers & Archer, this volume) with the Ngama Local Fauna from the Tirari Desert which Woodburne et al. (1993) have shown to be late Oligocene, about 24 to 26 My.

ETYMOLOGY. For Patrick Couper, Queensland Museum, for his assistance during the course of this research.

DESCRIPTION. The holotype is a fragment of a right dentary consisting of the entire horizontal ramus, most of the angular process and portion of the ascending ramus to the level of the damaged condyle (Fig. 1 A, B). Dorsal edge of the diastema delineated by a ridge with matrix-filled alveolus for a very small I₂ or analogous tooth at anterior end. Horizontal ramus twisted, with mesial surface inclined slightly dorsally below P₃ and slightly ventrally below M₄. Mandibular symphysis extending as far posteriorly as the level of the anterior margin of P₃. On the buccal surface the anterior mental foramen located below and slightly anterior to P₃, with a much smaller posterior mental foramen below the hypolophid of M₂. Horizontal ramus deepest below M₁, with its zone of most ventral protrusion below M₃. Ventral margin straightest below P₃-M₃, curving upwards below the diastema and more steeply so posterior to M₃. Buccal margin of the masseteric fossa straight so that the entrance to the masseteric canal is 'D' shaped in cross section. Ventral margin of the masseteric fossa low on the ramus, well below the level of the molar row. Inferior dental canal recessed into the lingual wall of the masseteric canal but not partitioned from it. Because of the confluence of the two canals, forward extent of the penetration of the masseter difficult to determine, but the gradient of anterior canal constriction suggesting insertion no further forward than M₃. Lingual border of the angular process in the same vertical plane as the lingual margin of the horizontal ramus but the angular process extending more posteriorly than the

ramus. Large portion of the floor of the pterygoid fossa lost.

Ascending ramus rising at 100° relative to the plane of the molar row. Condyle situated 9.4 mm above the molar row, a transversely elongate structure, broader lingually, tapering to the buccal side, obliquely inclined to the plane of the ascending ramus.

Dentition. Molar row straight in both occlusal and lateral view. P₃ flexed slightly buccally out of alignment with molar row. Occlusal surfaces of anterior molar lophids inclined slightly buccally. Those of more central molars more or less horizontal. Hypolophid of M₄ inclined lingually. Slight increase in molar size posteriorly.

P₃ gracile, short and blade-like with horizontal occlusal margin. In occlusal view with an elliptical outline with the occlusal crest occupying approximate midline, although curving lingually posteriorly. Five cuspids, of which most posterior largest, occupying the occlusal crest. Lingual and buccal transcrisids associated with each cuspid, although those on lingual surface partly obscured by wear. Anterior and posterior margins of crown delineated by vertical cristids.

In occlusal view M₁ with a rounded anterior margin and lateral convexities low on the crown adjacent to the ends of interlophid valley. Protolophid shorter than hypolophid: protoconid positioned on approximate midline of tooth. Protoconid taller than metaconid, buttressed buccally by a protostylid about same height as metaconid. Paracristid running almost directly forward to anterior margin where it meets anterior edge of a precingulid which descends steeply to buccal margin of tooth. No anterior cingulid, trigonid basin open anterolingually. Cristid obliqua inclined slightly lingually, descending anterior face of the hypoconid, turning anteriorly to cross interlophid valley and terminating at base of protostylid.

Entoconid taller than hypoconid. Occlusal crest of hypolophid forming shallow 'V' with lingual arm steeper than buccal. Low point of hypolophid slightly lingual of midline. Preentocristid descending to interlophid valley floor from apex of entoconid. Wedge shaped prominence at posterior base of entoconid, interpreted here as a hypoconulid because its position corresponding to that occupied by hypoconulid in other marsupials and, as in these animals, contacted by the posthypocristid. Short, lingually displaced, diagonal posthypocristid and hypoconulid forming posterobuccal border of small fossette in poste-

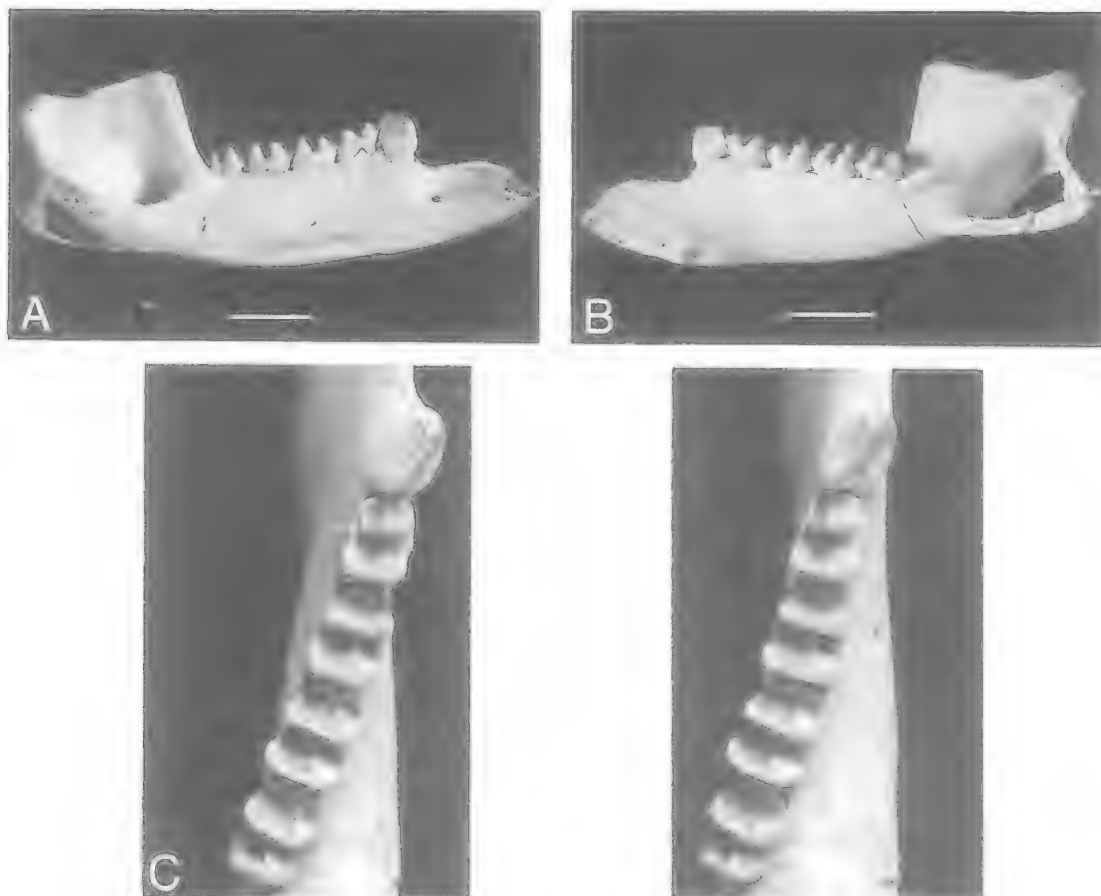


FIG. 1. QMF30401, Holotype of *Namaroo couperi* sp. nov. A, buccal view. B, lingual view. C, stereopair of occlusal view. Scales = 10mm.

rior face of entoconid. Rounded, lingual border probably representing postentocristid. From base of hypoconulid a hypocingulid extending across about half width of posterior base of hypolophid.

M₂ larger than M₁, approximately rectangular in outline, but with lateral convexities of crown base adjacent to ends of interlophid valley. Protolophid and hypolophid about equal in length, lingual cuspids taller than buccal cuspids. Occlusal margins of both lophids shallowly concave. Paracristid running anterolingually to anterior margin from which enamel has been lost, although sufficient remains to indicate that an anterior cingulid ran between paracristid and lingually positioned premetacristid. Short, steeply sloping precingulid extending from anterior end of paracristid to buccal margin of the tooth. Cristid obliqua running anterolingually across interlophid valley to join posterior base of pro-

tolophid at about midline. Preentocristid short, not reaching floor of interlophid valley. Postentocristid running vertically down posterior, lingual edge of entoconid to meet low and somewhat irregular hypocingulid which runs transversely across half width of the posterior face of hypolophid. No posthypocristid.

M₃ similar to M₂ but metaconid and hypoconid more nearly equal in height, hypocingulid less developed and cristid obliqua interrupted adjacent to base of protolophid.

M₄ differing from more anterior molars in the following: protolophid longer than hypolophid; no obvious convexities of crown base adjacent to ends of the interlophid valley; some wrinkling of the enamel within trigonid basin; precingulid less obvious; rounded postmetacristid descends posterior face of metaconid to floor of interlophid valley; cristid obliqua interrupted before contact-

TABLE 1. Dental parameters for QMF303401, Holotype of *Nambaroo couperi* sp. nov.

Cat. No.	P3			M ₁			M ₂			M ₃			M ₄		
	l	mw	h	l	pw	hw	l	pw	hw	l	pw	hw	l	pw	hw
QMF30401	5.2	2.9	3.9	5.2	2.6	3.3	5.4	3.5	3.9	5.6	3.9	4.1	5.4	3.8	3.6

ing base of protolophid and ridge of enamel runs transversely across floor of the interlophid valley from anterior end of cristid obliqua to buccal margin; hypoconid taller than entoconid (which is slightly damaged); no distinct postentoeristid; hypocingulid in form of rounded, transverse prominence crossing posterior face of hypolophid.

DISCUSSION. *N. couperi* is similar in size to *N. saltavus*, *N. tarrinyeri* and *N. novus* which were described by Flannery & Rich (1986) from the Tarkarooloo Local Fauna of South Australia. Apart from the plesiomorphic hypoconulid, *N. couperi* is in other aspects of talonid morphology, more derived than *N. saltavus*. It lacks a postentoeristid which is present in *N. saltavus*, and has a well-developed hypocingulid crossing buccally from the hypoconulid on the posterior base of the hypolophid, present also in *N. tarrinyeri* and *N. novus* but undeveloped in *N. saltavus*. The M₁ cristid obliqua contacts the protostylid of *N. couperi* as it does in *N. saltavus*, a condition which Flannery & Rich (1986) considered plesiomorphic for macropodoids. In *N. novus* the cristid obliqua contacts the base of the protoconid and in *N. tarrinyeri* the cristid obliqua

bifurcates and contacts both protostylid and protoconid. M₁ trigonid morphology in *N. couperi* is most similar to *N. novus* in that both have an anteriorly directed paraeristid, lack a paraconid and have a protostylid which is closely associated with the protoconid.

Wururoo gen. nov.

TYPE SPECIES. *Wururoo dayamayi* sp. nov.

DIAGNOSIS. Balbarines with a large, trenchant P₃ and a posterobuccally inclined enamel ridge (the 'protostylid crest') descending from the apex of the protoconid of M₁.

ETYMOLOGY. Gulf coast aboriginal *wuru*, a long time ago (Breen, 1981), and *roo* a common Australian diminutive for 'kangaroo'. Masculine.

Wururoo dayamayi sp. nov. (Figs 3, 4, 5B; Table 2)

DIAGNOSIS. As for genus.

MATERIAL. Holotype QMF19820. A fragment of the horizontal ramus of a right dentary, extending from the anterior end of the diastema to the posterior of the molar row and preserving P₃ and M₁₋₄. from White Hunter Site, Hal's Hill, D Site Plateau, which has been correlated (Myers & Archer, 1997) with the Ngama Local Fauna from the Tirari Desert which Woodburne et al. (1993) have shown to be late Oligocene, about 24 to 26My.

ETYMOLOGY. Waanyi *daya*, chop; *mayi* tooth, for the tall, robust plagiaulacoid premolar of the holotype.

DESCRIPTION. Only small portion of anterior margin of ascending ramus present, remainder of dentary posterior to M₄ lost. Horizontal ramus deepest below M₃/M₄, tapering gently anteriorly, ramus twisted so that mesial face inclines dorsally below P₃ and slightly ventrally below M₄. Low ridge running length of dorsal margin of very short diastema. Mental foramen well below and slightly anterior to P₃, small posterior mental foramen below hypolophid of M₂. Masseteric canal elliptical in cross section, extending forward at least as far as anterior of M₂, from which position anterior of canal blocked by undissolved

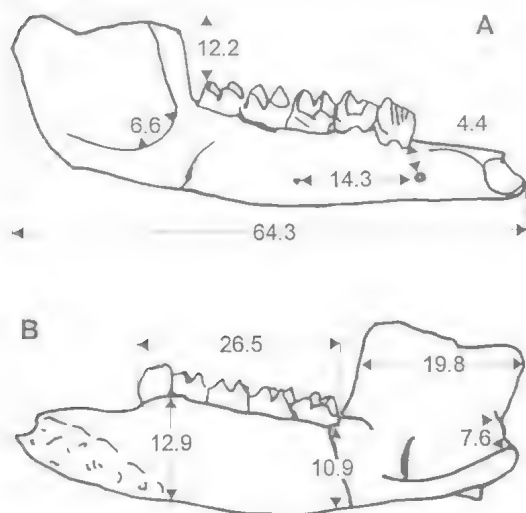


FIG. 2. Dimensions of QMF30401, holotype of *Nambaroo couperi* sp. nov. A, buccal view. B, lingual view.

matrix. A narrow canal, the inferior dental canal or branch thereof, partitioned from lingual side of masseteric canal by thin lamina of bone anterior to M4. Mandibular symphysis extending posteriorly to below mid point of P3. Molar row concave in lateral view and straight in occlusal view. Molar size increasing from M1 to M3 but M4 a little smaller than M3.

Dentition. P3 large, robust, plagiaulacoid, occlusal edge well above occlusal plane of molar row, long axis flexed slightly buccally out of alignment with line of molar row. Viewed occlusally with a convex buccal margin and slightly concave lingual margin. Lingual face of crown inclined at steeper angle than is buccal. Occlusal margin on approximate midline for most of length, but slightly lingually displaced at posterior end. Six cuspids on occlusal margin, all but most posterior having associated lingual and buccal transcrisids. Crisids descending anterior and posterior margins of crown from corresponding cuspids.

M1 roughly rectangular in occlusal outline but with distinct lingual convexity in crown base adjacent to interlophid valley. Anterior margin abutting posterior buccal margin of P3. Protolophid markedly shorter than hypolophid with protoconid set on approximate midline. Lingual cuspids positioned closer to margin and with steeper lateral walls than buccal cuspids. Both protolophid and hypolophid crests concave anteriorly, posterior faces of both lophids vertical. Protoconid taller than metaconid. Paracristid straight but anterolingually inclined as descends from protoconid apex to a prominence positioned just posterior to anterior margin. A short but clearly defined ridge is directed lingually from apex of prominence, ending abruptly anterior to midpoint of protolophid. While the prominence may represent the paraconid, an alternative view preferred here is that this ridge represents a lingual extension of the paracristid, and its termination the paraconid (see Fig. 7c). Line of paracristid continued by a ridge running anteriorly from anterior prominence for very short distance and at steeper angle to anterior margin. From here a continuous ridge descends ventrobuccally on anterior margin, forming border of narrow precingulid which ends before reaching buccal margin. No premetacristid or postmetacristid. An enamel ridge, the 'protostylid crest' descends posterobuccally from apex of protoconid for about half height of that cusp where it is contacted by ascending, anterior

portion of cristid obliqua. Cristid obliqua descends anterolingually from apex of hypoconid before turning anteriorly to cross wide interlophid valley and ascend diagonally on posterior of protoconid.

Entoconid taller than hypoconid which shows evidence of wear: enamel breached on lingual side of apex. Preentocristid descends directly anteriorly from apex of entoconid to floor of interlophid valley. Posthypocristid short, extremely lingually displaced, originating at lowest point of hypolophid crest, closer to entoconid than hypoconid, descending ventrolingually to meet postentocristid just above base of entoconid. Inverted triangular fossette enclosed laterally by posthypocristid and postentocristid. Below junction of postentocristid and posthypocristid is short, prominent enamel ridge, descending at different angle to postentocristid and which may represent a reduced hypoconulid. This ridge forms lingual margin of broad, horizontal hypocingulid extending across two-thirds of base of hypolophid.

Broad wear facets on posterior face of protolophid extend across link between protostylid crest and cristid obliqua; similar facets on posterior face of hypolophid extend across posthypocristid. Facets bear fine vertical striae.

M2 rectangular in occlusal outline but with slight concavity of lingual margin adjacent to end of interlophid valley. Protolophid and hypolophid subequal in length, occlusal crest of hypolophid slightly more anteriorly concave than that of protolophid. Lingual cuspids set closer to lateral margin and with steeper lateral walls than buccal cuspids. Metaconid taller than protoconid which shows evidence of wear: enamel breached lingually adjacent to apex. Paracristid directed anterolingually as descends from protoconid apex to anterior margin. Prominent premetacristid runs slightly buccally as descends from metaconid apex to anterior margin. Short, broad anterior cingulid enclosed between these cristids. Short precingulid buccal to paracristid. In posterior view occlusal crest of protolophid forms shallow 'V' with low point located closer to protoconid than metaconid. Cristid obliqua forms thick enamel ridge as crosses interlophid valley, tapering somewhat anteriorly as ascends short distance on lingual side of posterior face of protoconid. No postmetacristid or preentocristid: broad interlophid valley widely open lingually. Floor of interlophid valley considerably more elevated on lingual side of cristid obliqua than on buccal side which slopes steeply towards crown

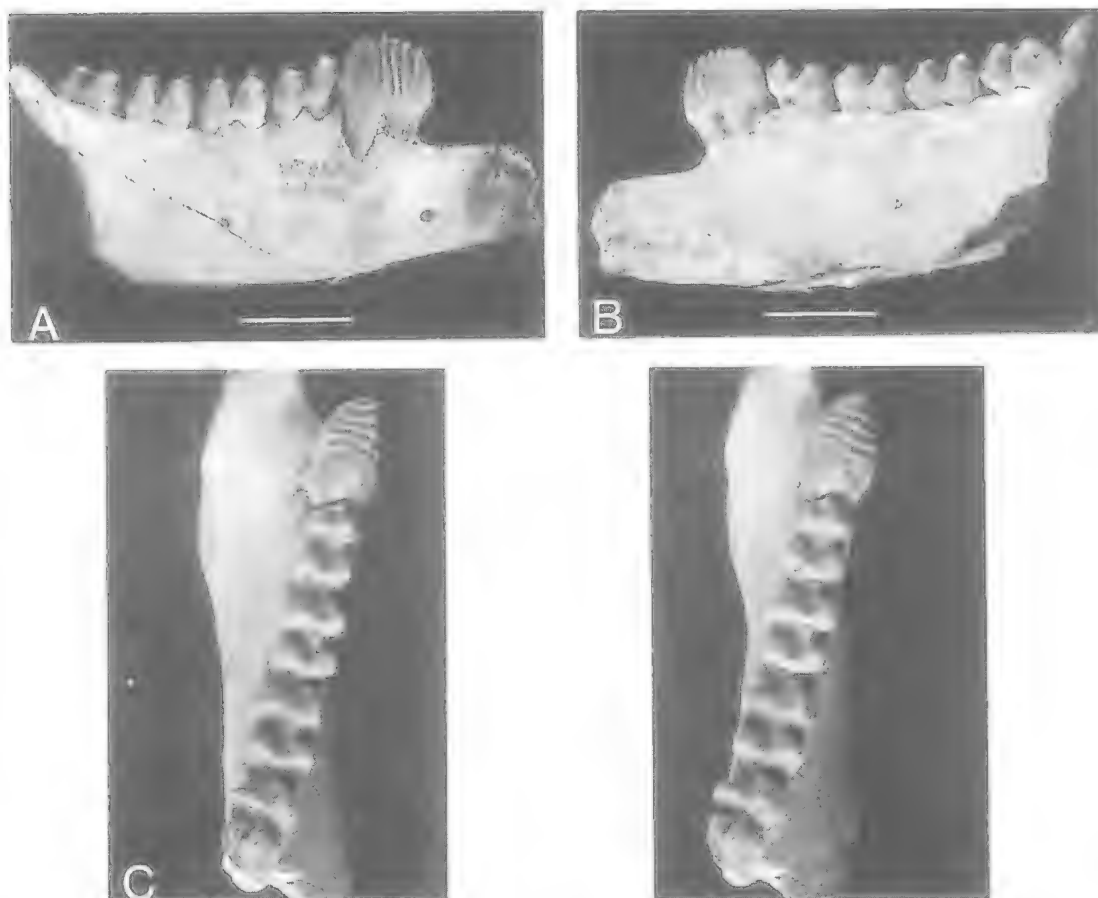


FIG. 3. QMF19820, Holotype of *Wururoo dayamayi* gen. et sp. nov. A, buccal view. B, lingual view. C, stereopair of occlusal view. Scales = 10mm. AR number is an informal system used in the Vertebrate Palaeontology Laboratory, University of New South Wales.

base. Entoconid and hypoconid subequal in height. No posthypocristid. Thick ridge of postentocristid continuous with similarly prominent hypocingulid which descends slightly ventrally as crosses posterior base of the hypolophid.

M₃ with longer anterior cingulid, lingual cusps taller than buccal cusps, protolophid slightly longer than hypolophid and thickened ridge, representing remnant of posthypocristid, descending vertically from low point of occlusal crest on posterior face of hypolophid. Less worn than is M₂. Cristid obliqua can be seen to arise from more anterolingual position relative to apex of the hypoconid.

M₄ smaller than M₃ with much narrower anterior cingulid. Lacking precingulid buccal to paracristid. Hypolophid markedly shorter than protolophid. Metaconid taller than protoconid, crest of protolophid formed chiefly by buccal

crest from apex of metaconid, descending to meet lingual flank of protoconid at a point directly in line with anterior end of cristid obliqua. Cristid obliqua originates lingual to hypoconid apex and runs directly anteriorly across interlophid valley. Hypoconid and entoconid subequal in height but entoconid set somewhat anterior to hypoconid. Apex of entoconid damaged during life and broken edges of enamel subsequently smoothed as a result of wear. Hypolophid crest with a narrow V-shape in posterior view with lingual arm running slightly anteriorly towards damaged apex of entoconid. No preentocristid but very thick postentocristid running ventrobuccally on posterior face of entoconid, merging with equally prominent hypocingulid which crosses half width of hypolophid base.

TABLE 2. Dental parameters for QMF19820, Holotype of *Wururoo dayamayi* gen. et sp. nov.

Cat. No.	P3			M ₁			M ₂			M ₃			M ₄		
	l	mw	h	l	pw	hw	l	pw	hw	l	pw	hw	l	pw	hw
QMF19820	8.6	4.9	6.7	5.9	4.1	4.2	6.5	4.8	4.5	6.9	5.1	4.7	6.7	4.3	4.1

DISCUSSION. P₃ is much larger and more massive than that in *Nambaroo* or *Ganawamaya* Cooke, 1992, and is similar to that in undescribed Riversleigh species of *Balbaroo*. The large P₃ in the latter balbarines is more similar in profile and size relative to molars to propleopines and hypsiprimnodontines than to macropodids. The diastema in *W. dayamayi* is also much shorter than in *Nambaroo* or *Ganawamaya*. The shorter diastema and markedly more robust P₃ may be indicative of a greater reliance on the use of premolar shearing action in food collection and/or processing. The similarity of plagiaulacoid premolars in more derived balbarines, propleopines and hypsiprimnodontines may be the result of convergence in species placing a similar emphasis on premolar shearing. However, premolars in these groups are similar in form to those of phalangerids and it is likely that the palgiulacoid premolar form is plesiomorphic for macropodoids. If robust, plagiaulacoid premolars are plesiomorphic, within Balbarinae the markedly more gracile premolars of *Nambaroo* and *Ganawamaya* would represent an apomorphy for a clade containing these two genera.

The lingually displaced M₁ posthypocristid seen in *W. dayamayi* is also present in species of *Nambaroo* and in *Ganawamaya aediculis* Cooke, 1992. Its widespread occurrence among plesiomorphic balbarines supports the view of Flannery & Rich (1986), that lingual displacement of the posthypocristid has played an important role in hypolophid formation in Balbarinae. The connection of the cristid obliqua to the pro-

tostylid crest resembles the connection between the cristid obliqua and the discrete protostylid of *Nambaroo saltavus* as noted by Flannery & Rich (1986), and suggested by them to represent the plesiomorphic state of this character in macropodids.

The M₁ precingulid in other undescribed plesiomorphic balbarine species (pers. obs.) receives the posterolingual cusplule of P₃. The precingulid is low in *W. dayamayi*, suggesting that a prominent posterolingual cusplid is to be expected on its P₃. The lingual ridge associated with the M₁ paraconid forms the margin of a small anterior cingulid which receives the posterior end of the P₃ occlusal margin, as indicated by signs of wear on the posterior face of the ridge. The broad wear facets on the posterior faces of the M₁ lophids indicate broad contact with the lophids of M¹ while the orientation of the striae indicate greater vertical rather than lateral relative movement between lophids and lophids.

CUSPID HOMOLGY AND EVOLUTION OF LOWER MOLAR MORPHOLOGY IN BALBARINAE

Differing views of cuspid homology and evolution of lower molar morphology among macropodoids are examined and alternative hypotheses proposed to determine homology of structures on lower molars of plesiomorphic balbarines from Riversleigh and to elucidate the course of molar evolution within Balbarinae. Since interpretations of cuspid homology in *Hypsiprymnodon* have been central to wider arguments pertaining to macropodoid molar evolution, such interpretations of previous authors are reviewed first and a new interpretation presented which incorporates evidence provided by the new species described herein.

The posterobuccal protostylid crest in *W. dayamayi* is very similar to that which descends from the dominant trigonid cuspid to a tiny buccal cuspid in dP₃ of *Hypsiprymnodon moschatus*. Ride (1961) identified the dominant cuspid as the metaconid and the tiny cuspid as the protoconid, but has since modified this interpretation (Ride, 1993), considering the central trigonid cuspid posterior to the paraconid on dP₃ to be a

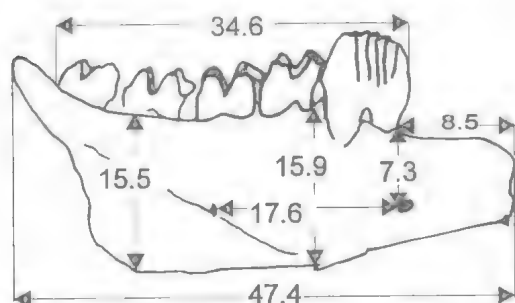


FIG. 4. Dimensions of QMF19820, holotype of *Wururoo dayamayi* gen. et sp. nov., buccal view.

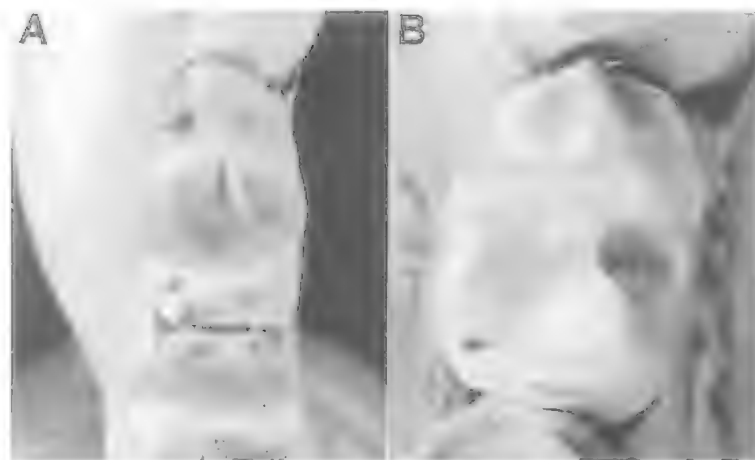


FIG. 5. Posterior occlusal views of M_1 . A, QMF303401, holotype of *Nambaroo couperi* sp. nov. B, QMF19820, holotype of *Wururoo dayamayi* gen. et sp. nov..

parametaconid and the small cuspid posterobuccal to this to be the protoconid, with the normal relationship of protoconid, metaconid and paraconid preserved on M_1 , the parametaconid having been lost in this tooth.

Archer (1978) raised the possibility that the anterobuccal cusp in M_1 (his M_2) of *H. moschatus* (and other macropodoids) may be 'the homologue of the phascolarctid protostylid and not the protoconid' and further that 'the tiny cusp observed by Ride (1961) on M_1 (Ride's dP_4 and here dP_3) of *Hypsiprimnodon* may be the serial homologue of this protostylid'. Archer & Flannery (1985) and Flannery & Rich (1986) also identified the posterobuccal cuspid of the M_1 trigonid of *H. moschatus* as the protostylid having here an anterior cristid descending to the anterior margin, and the cuspid lingual to this, also with an anterior cristid, as the protoconid, the metaconid being displaced posterolingually.

The interpretation of trigonid cuspid homology on dP_3 offered by Archer (1978) is accepted here but none of the above views regarding M_1 trigonid morphology in *H. moschatus* are upheld. For reasons explained below, the most buccal cuspid-like structure associated with the protolophid is accepted as the protostylid but the lingual cuspid of the protolophid is regarded as the metaconid.

As Ride (1993) noted, constraints imposed by functional interactions with premolars can alter the topography of teeth at the premolar/molar boundary, so cuspid homology of M_1 in *H. moschatus* has been examined with reference to

more posterior molars. Molars posterior to M_1 have a buccally positioned protoconid which has a paracristid running to the anterior margin. The metaconid of these molars is lingually positioned and has an associated premetacristid. Both cristids are present on M_1 and bear the same relationship to each other as they do on more posterior molars. The metaconid is distinct but the protoconid, from which the paracristid originates, may be considerably reduced and is more centrally positioned, the trigonid thereby becoming laterally compressed in a manner closely resembling that seen in balbarines. In unworn *H.*

moschatus specimens (QMJ10233, QMJ9327, QMJ145), the paracristid originates from a slight elevation, interpreted here as the reduced protoconid (Fig. 6F). A posterobuccal crest links this to a larger cuspid which is thus the protostylid in the sense in which the term is used by Van Valen (1966), and Butler (1978): it occurs in the same position as the protostylid of other diprotodont marsupials, e.g., pseudocheirids and phascolarctids and *Nambaroo*, a position in which it fulfils the function ascribed to it by Butler (1978), i. e., 'to shear against the anterolingual surface of the paracone of the corresponding upper tooth' (a function which could not be fulfilled by the 'one or more protostylids' indicated by Ride (1993), as occurring on the precingulid anterobuccal to the M_1 trigonid in the propleopines, *Jackmahoneya* and *Propleopus*).

Ride (1993) indicated 3 cuspids immediately posterior to the paraconid of dP_3 of *H. moschatus*: the large, central cuspid identified as the parametaconid, a posterolingual metaconid and a very small posterobuccal protoconid. The posterolingual cuspid is accepted here as the metaconid but since the large, central cuspid has a cristid running anteriorly from its apex toward the paraconid, the cuspid is here regarded (as it was by Archer, 1978) as the protoconid, its cristid as the paracristid and the small posterobuccal cuspid as the protostylid, homologous with that which also occurs on dP_3 in undescribed Riversleigh specimens of *Nambaroo* (pers. obs.), the protostylid on M_1 of *H. moschatus* and the

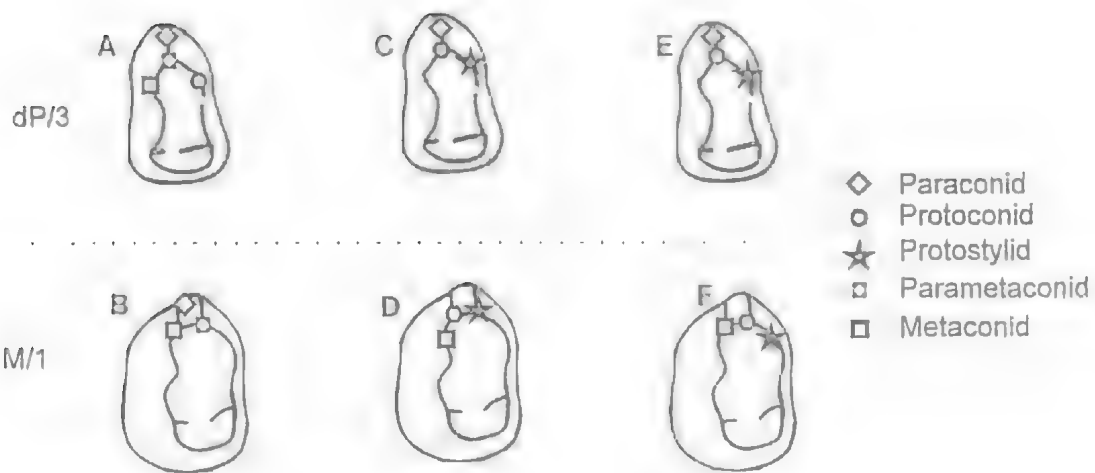


FIG. 6. Interpretations of trigonid cuspid homology in *Hypsiprymnodon moschatus*. A & B, Ride (1993). C, Archer (1978). D, Archer & Flannery (1985). E, F, Cooke (herein).

protostylid crest on M_1 of *Wururoo* and on dP_3 of bulungamayine species (Cooke, 1997).

The homology of the buccal cuspid on the M_1 protolophid of propleopines is less clear. Ride (1993) labelled this cuspid as the protoconid and the cuspid immediately lingual to it as a neomorph, the parametaconid. Flannery & Archer (1985) labelled the buccal cuspid as the protostylid and the cuspid immediately lingual to it as the protoconid. While it is clear that the protostylid, as a discrete cuspid or as a protostylid crest, is common among plesiomorphic macropodoids, it is unusual in this group for it to have acquired a cristid mimicking the paracristid in linking to the anterior cingulid. If Flannery & Archer are correct, this would constitute a synapomorphy for propleopines as would the neomorphic parametaconid in the interpretation of Ride.

The suggestion of Archer & Flannery (1985) that the buccal cuspid of the protolophid in M_1 of propleopines and potorines was the protostylid and that the metaconid was lost in potorines but retained in propleopines was enlarged upon by Flannery & Rich (1986). They suggested that in potoroids the protostylid formed the buccal protolophid cuspid and the protoconid the lingual cuspid, in contradistinction to macropodids in which the protostylid is lost and the buccal cuspid is the protoconid and the lingual cuspid the metaconid (lost in potoroids other than propleopines). The plesiomorphic balbarines, *Nambaroo*, *Wururoo* and *Ganawamaya* certainly

indicate that the protostylid has been reduced and ultimately lost in balbarines, however there is less evidence to support a belief that it has been retained in potoroids. The M_1 (Cooke, 1997) protostylid of *Palaeopotorous priscus* Flannery & Rich, 1986, bears a similar relationship to the protoconid and cristid obliqua as does that of *H. moschatus*, exhibiting a condition intermediate between the distinct cuspid of the protostylid of *Nambaroo* and the protostylid crest of *W. dayamayi*. It thus may represent an early stage in the reduction of the protostylid among potoroids. In the proposals of cusp homology in macropodids and potoroids referred to above, the condition occurring in *H. moschatus* is crucial because it is used in both cases to represent the intermediate condition between a phalangerid ancestor and more derived potoroids. If, as has been proposed here, the reduced cuspid from which the paracristid originates on the short M_1 protolophid of *H. moschatus* is the protoconid, then there is no reason to suppose that this is not also the case in other potoroids and the sequence, *Palaeopotorous* - *Hypsiprymnodon* - *Potorous*, used by Flannery & Rich (1986) to illustrate their argument can be taken as indicating a transition involving reduction of the protostylid.

The protostylid is also exhibited in varying degrees of development within phalangerids. A very similar structure to the M_1 protostylid crest of *W. dayamayi* occurs in *Phalanger intercastellanus* and joins the cristid obliqua. In *Trichosurus vulpecula* there is a straight ridge

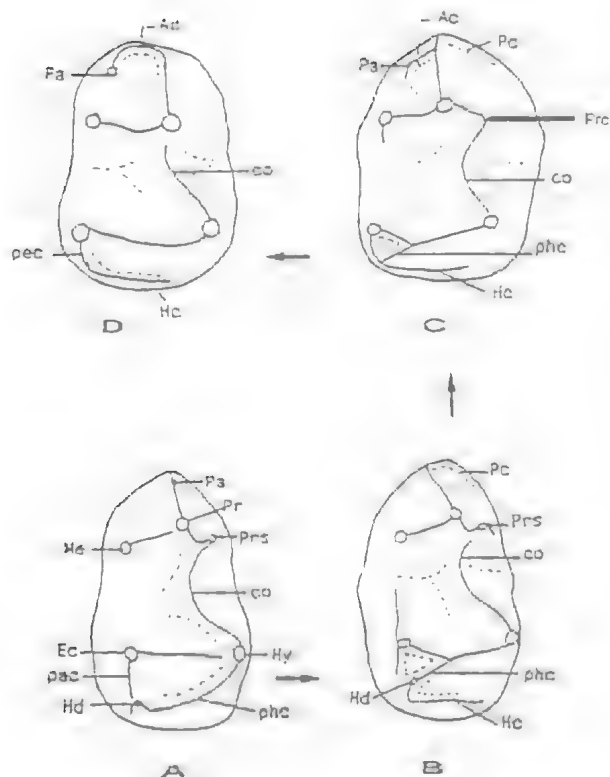


FIG. 7. Evolution of lower molar morphology in balbarines illustrated by RM₁. A, hypothetical macropodoid ancestor. B, *Nambaroo couperi*. C, *Wururoo dayamai*. D, *Balbaroo* grade. Abbreviations: Ac=anterior cingulid; co=cristid obliqua; Ec=entoconid; Hc=hypocingulid; Hd=hypoconulid; Hy=hypoconid; Me=metaconid; Pa=paraconid; Pc=precingulid; pec=postentoconid; phc=posthypocristid; Pr=protoconid; Prs=protostylid; pre=protostylid crest.

descending posterobuccally to the base of the protoconid where it links to the cristid obliqua. In *T. caninus* there is a ridge on the protoconid resembling that in *T. vulpecula*, but it does not contact the cristid obliqua which independently ascends the posterior face of the protoconid. Flannery & Rich (1986) indicate a discrete protostylid in *Phalanger vestitus* and a similar situation occurs in *Spiloglossus maculatus*, but in some specimens of this species the protostylid may be reduced to a ridge on the posterobuccal flank of the protoconid. Flannery & Archer (1987) suggest a protostylid on M₁ in *Strigocuscus reidi* and *Trichosurus dicksoni*, both from System C sites at Riversleigh.

It would appear that the genetic potential for the formation of a protostylid is widespread among phalangeridans and may be considered as

plesiomorphic for the group. In pseudocheirids among Petauroidea and *Nambaroo* among Macropodoidea the protostylid is fully developed but in most phalangerids and in *Palaeopotorous*, *Hypsiprionodon* and *Wururoo* the potential is not as fully expressed. This expression has independently been suppressed among more derived macropodoids (with the possible exception of propleopines) and other phalangeridans.

Wururoo is more derived than *Nambaroo* in terms of M₁ morphology: the protostylid has been reduced, a neomorphic anterior cingulid has begun to form and the trigonid basin has become partly enclosed. *Nambaroo* and *W. dayamai* indicate initial stages of a trend among balbarines towards the development of an anterior cingulid and the enclosure of the trigonid basin. Concomitant with this trend is a decrease in the relative importance of the precingulid which occupies much of the M₁ anterior margin in plesiomorphic species such as *N. couperi*.

Hypolophid formation in balbarines proceeded as outlined by Flannery & Rich (1986), involving elevation and lingual displacement of the posthypocristid which contributes a buccal component to the hypolophid, the lingual component contributed by a buccally directed cristid from the entoconid. The latter cristid is not necessarily a neomorphic 'entohypocristid' (Ride, 1993). However, the hypoconulid on the M₁ of *N. couperi* and its apparent presence in a reduced form on M₁ of *W. dayamai* indicates the additional involvement of this cuspid in hypolophid

formation in plesiomorphic balbarines (Fig. 7). The hypoconulid in such forms is contacted by a lingually displaced, diagonal posthypocristid. An inverted triangular fossette occurs on the lingual posterior face of the hypolophid, bounded by the posthypocristid and the postentoconid (when present). A shallow fossette develops buccal to the posthypocristid and a neomorphic cingulid, the hypocingulid according to the definition of Butler (1990), develops transversely across the posterior base of the hypolophid from the hypoconulid or, when that structure has been lost, from the ventral end of the posthypocristid, as in *N. saltavus*. The posthypocristid is lost in more derived species such as those of *Balbaroo* in which the postentoconid links to a transverse,

posterior cingulid homologous with the hypocingulid.

The modification offered above to the hypothesis of Flannery & Rich has been extended by Ride (1993) to macropodoids in general but I apply it only to balbarines. The bilophodont lower molar morphology of bulungamayines is derived from a bunolophodont ancestral form by different means to those outlined above (Cooke, 1997) and clearly indicates independent evolution of lophodonty within this group. However, a hypoconulid positioned low on the posterior, lingual face of the hypolophid and associated with a posthypocristid, is the probable plesiomorphic condition for all macropodoids. The basal macropodoid may well have had a bunolophodont lower molar morphology similar to that of *Palaeopotorous* or of phalangerids, but with a more distinct protostylid buccal to the protoconid and a hypoconulid contacted by the posthypocristid at the posterior base of the entoconid. The lingual component of the balbarine hypolophid would represent a reduction of the buccal cristid of the entoconid which forms the transverse posterior lophid of bunolophodont macropodoids.

The hypoconulid in plesiomorphic balbarines and its absence in any known potoroids of comparable age suggests that balbarines diverged early from the main stem of macropodoid evolution and independently and probably rapidly evolved lophodonty, the better to exploit a herbivore niche. The combination of plesiomorphic dental characters present in balbarines, including lateral compression of the M₁ trigonid and the presence of both a hypoconulid and protostylid on this tooth, contrasts markedly with the absence of such characters in bulungamayines. There has been parallel (and probably later) evolution of lophodonty within Bulungamayinae and the absence of plesiomorphic molar characters such as those indicated above, suggests that bulungamayines may be more likely to be ancestral to the highly derived macropodids.

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NEW MIOCENE BULUNGAMAYINE KANGAROOS (MARSUPIALIA:
POTOROIDAE) FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

B. N. COOKE

Cooke, B.N. 1997 06 30: New Miocene bulungamayine kangaroos (Marsupialia: Potoroidae) from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 281-294, Brisbane. ISSN 0079-8835.

Nowidgee matrix gen. et sp. nov. and *Gangurua bilumina* gen. et sp. nov. are described from freshwater Miocene System B limestone at Riversleigh, NW Queensland. Subfamilial diagnosis of Bulungamayinae is emended. The new species indicate that lophodonty was achieved in bulungamayines by a different process from that in balbarines. Similarities in dental morphology between bulungamayines and late Miocene macropodids suggest that Bulungamayinae is ancestral to Macropodidae. □ Riversleigh, kangaroo, balbarines, Bulungamayinae, lophodonty.

B.N. Cooke, School of Life Science, Queensland University of Technology, GPO Box 2434, Brisbane, Queensland 4001, Australia; 17 December 1996.

Rat-kangaroos or potoroids, in the sense of Archer & Bartholomai (1978) and Bartholomai (1978), were unknown in the pre-Pliocene fossil record of Australia until Archer (1979) described *Wabularoo naughtoni* as an enigmatic, lophodont kangaroo from the Riversleigh Local Fauna of the Carl Creek Limestone. Flannery et al. (1982) described *Bulungamaya delicata* from the Carl Creek Limestone and placed it and *W. naughtoni* in the potoroid Bulungamayinae. *Gumardee pascuali*, also from the Carl Creek Limestone was described in the same paper but placed in the Potoroinae. More recent additions to the record of potoroides include *Wakiewakie lawsoni* Woodburne, 1984 and *Purtia mosaicus* Case, 1984, from the Ngapakaldi Local Fauna of South Australia and *Bettongia moyesi* Flannery & Archer, 1987, from Two Trees Site at Riversleigh. Flannery & Rich (1986) described *Gumardee* and indeterminate potoroides from the Tarkooloo Local Fauna of South Australia.

Archer & Flannery (1985) erected *Propleopinae* for *Ekaladeta ima*, a giant rat kangaroo from Gag Site at Riversleigh and Pleistocene and Pliocene species of *Propleopus*. Flannery & Archer (1987) described *Hypsiprimnodon bartholomaii* from the Gag Site at Riversleigh and Flannery & Rich (1986) reported hypsiprimnodontine material from the Tarkooloo Local Fauna. Palaeopotoroidae Flannery & Rich, 1986 accommodates *Palaeopotorous priscus* from the Tarkooloo Local Fauna.

The diversity of pre-Pliocene potoroids is such that only 2 of the more recently discovered species have been assigned to existing genera and 3 new subfamilies have been proposed. Of these

Bulungamayinae Flannery et al., 1982, has attracted most discussion. Woodburne (1984) and Case (1984) argued that the lophodont bulungamayines *W. naughtoni* and *B. delicata* share characteristics with plesiomorphic macropodids (their macropodines) such as *Dorcopsoides fossilis* Woodburne, 1967, *Dorcopsis* and *Dorcopsulus* and should be included in Macropodidae (their Macropodinae). They also argued a similar placement of *Gumardee*. Flannery et al. (1984) identified synapomorphies which they considered united potoroids in a monophyletic group and defended their placement of bulungamayines and *G. pascuali* within Potoroidae on the basis of several of those derived states. Flannery & Archer (1987a, b) demonstrated that one suggested synapomorphic character, squamosal-frontal contact on the lateral wall of the cranium, is not universal within the group and could no longer be considered as a potoroid synapomorphy. The state of this character is unknown in new bulungamayine material described below.

The new species are similar in size and have similar premolar morphology to that of *B. delicata* and together with that species represent a sequence which reveals much about the evolution of lophodonty within Bulungamayinae.

METHODS

Molar homology follows Luckett (1993), premolar homology follows Flower (1867). Dental descriptive terminology is principally that used by Archer (1984) but with some terms adopted from Szalay (1969) and Ride (1993). In upper

molars the term, 'paracingulum' is used to indicate an anterior cingulum bounded laterally by the preparaecrista and preprotocrista as indicated in Szalay (1969). Ride used 'precingulum' for this structure. I use 'precingulum' for an anterior cingulum extending lingually from the preprotocrista, following Szalay. This structure was referred to by Ride as the 'anterolingual cingulum'. 'Metacingulum' is used for a posterior cingulum bounded posterolingually by the postmetaconule crista; 'paracrista' and 'metacrista' are used for the lingually directed, loph-forming cristae from the paracone and metacone, respectively. Use of the latter term in this manner is a departure from Szalay who uses 'metacrista' synonymously with 'postmetaerista'. 'Postmetacrista' is used here in the sense of Archer (1984).

Cusp homology of upper molars is that of Tedford & Woodburne (1987), with the posterior buccal and lingual cusps designated as metacone and metaconule respectively, and the cuspule between these as the neometaconule. Suprageneric classification follows Aplin & Archer (1987). Material is housed in the Queensland Museum (QMF). Measurements are in millimetres.

SYSTEMATICS

Superfamily MACROPODOIDEA Gray, 1821
Family POTOROIDAE Gray, 1821
Subfamily BULUNGAMAYINAE
Flannery, Archer & Plane 1982, emend.
Cooke, 1997

Bulungamayines have a buccally expanded masseteric canal confluent over its length with the inferior dental canal, the common canal penetrating deeply within the dentary below the molar row. The digastric process of the dentary is expanded so that the ventral margin of the dentary is convex below the molar row. I₁ has enamel confined to the buccal surface but extensive on that surface and not confined to the ventral portion as it is in potorines. Ventral and dorsal enamel flanges are present on I₁. P₃ is elongate with many fine transcrists and a bulbous base. A small tooth, I₂ but which may be a small canine, is just posterior to the dorsal margin of the I₁ alveolus. Molar teeth may be bunolophodont or lophodont as defined by Flannery et al. (1984).

Bulungamayines differ from hypsiprimnodontines and propleopines by having an elongate P₃ whose occlusal margin in lateral view is straight or concave, rather than a plagiaulacoid P₃

with a convex occlusal margin. They differ from potorines by having much more bulbous premolars, by having an I₂ and a much more extensive area of enamel on the buccal surface of I₁. They differ from palaeopotorines by lacking a distinct protostylid on M₁.

REMARKS. Type specimens of bulungamayines erected herein are far more complete than those of previously described species and reveal details of anatomical and dental features absent in the holotypes of *Bulungamaya delicata* and *Wabularoo naughtyi*. This additional information forces the above subfamily revision.

Nowidgee gen. nov.

TYPE SPECIES. *Nowidgee matrix* sp. nov.

DIAGNOSIS. Bulungamayine with bunolophodont molars. Upper molars with a large stylar cusp C extending posteriorly to close the buccal end of the interloph region.

ETYMOLOGY. Waaanyi (as spoken by Ivy Stinken, formerly of Riversleigh Station) *Nowidgee*, grandmother.

Nowidgee matrix sp. nov. (Figs 1, 2; Table 1)

DIAGNOSIS. As for the genus.

MATERIAL EXAMINED. Holotype QMF30390, from Camel Sputum, Godthelp's Hill, D-Site Plateau. Paratypes QMF19961, 20255, 22761, 30393, 30394, 30395 from Camel Sputum Site, QMF19937, 20069, 20080, 30391 from Wayne's Wok Site, Hal's Hill, D-Site Plateau. Both System B sites (Archer et al., 1989) of Miocene age.

ETYMOLOGY. Latin *matrix*, mother of an animal; refers to its ancestral position.

DESCRIPTION OF HOLOTYPE. Right dentary fragment of most of the horizontal ramus to the level of M₄ and part of the ascending ramus. I₁, P₃ and M₁₋₄ preserved. Ascending ramus at about 110° to occlusal plane of molar row. Masseteric canal confluent with inferior dental canal, making it difficult to assess extent of forward penetration of the masseter, but anterior wall of masseteric fossa extending anteriorly to about level of the M₃ protolophid. At this level diameter of common canal not greatly exceeding that of sulcus representing inferior dental canal in posterior, lingual wall of masseteric fossa. This suggests anterior portion of common canal occu-

plied chiefly by vessels associated with dental canal and masseter not passing much more anteriorly than this level. Masseteric fossa buccally expanded with flat surface for attachment of superficial layer of masseter at anteroventral border, extending dorsally on anteroheuccal margin of ascending ramus. Ventral margin of horizontal ramus gently convex with lowest point below M₂/M₃. Mental foramen just anterior to P₃, between root of I₁ and dorsal margin of the diastema; much smaller posterior mental foramen ventral to protolophid of M₂. Posteroventrally inclined buccinator sulcus between P₃ alveolar margin and posterior mental foramen. Diastema short, as long as P₃. Damage to I₁ alveolar margin obscuring I₂ or its alveolus (I₂ alveolus in QMF 19937). Mandibular symphysis extending posteriorly almost to level of P₃ posterior margin.

Dentition. Molar row straight in occlusal view, P₃ flexed slightly buccally out of alignment with it. In lateral view molar row concave; occlusal surfaces of M₂ and M₃ lying below line joining occlusal surfaces of M₁ and M₄. Effects of wear on molar teeth progressively less obvious towards posterior of molar row. Molar size increases from M₁-M₃ but M₃ larger than M₄.

I₁ broken at anterior end, depth uniform over preserved length, rising at approximately 20° relative to dorsal margin of horizontal ramus. Enamel confined to buccal side, has both dorsal and ventral enamel flanges, ventral being more strongly developed. Dorsal flange forms occlusal margin. Circular cross-section close to alveolus becoming more elliptical anteriorly.

P₃ blade-like, 50% longer than M₁. Occlusal outline semilunar with straight lingual margin and convex buccal margin. Occlusal crest slightly lingual to midline, flexes lingually at posterior end. Six small cuspids on occlusal margin anterior to longer, posterior cuspid. Transeristids associated with each of 6 minor cuspids and anterior and posterior margins of blade delineated by vertical cristids. Lingual surface of occlusal blade more steeply inclined than buccal.

M₁ almost square in occlusal outline but narrower anteriorly than posteriorly. Protolophid shorter than hypolophid; protoconid closer to midline than is hypoconid. Lingual cuspids taller, more sharply angular and closer to adjacent lateral margin than rounded, buccal counterparts which are also more worn. Lingual surfaces vertical, buccal surfaces more gently sloping. Protolophid formed by metaeristid descending buccally from metaconid apex to lingual flank of protoconid. Thick paraeristid running antero-

lingually from apex of protoconid to anterior margin. Short, broad anterior cingulid anterior to anterior face of protolophid, bounded buccally by paraeristid, lingually by anteriorly directed premetaeristid. Broad precingulid sloping steeply ventrally buccal to paraeristid. Sharply-defined postmetaeristid curving buccally from metaconid apex, descending to narrow interlophid valley. Anteriorly oriented preentocristid separated from ventral end of postmetaeristid by narrow cleft. Cristid obliqua very thick, descending anterolingually from apex of hypoconid to interlophid valley, then inclining buccally to apex of protoconid. Paraeristid and cristid obliqua form continuous longitudinal ridge extending from anterior margin to hypoconid. Hypolophid formed by buccal crest from the entoconid descending from entoconid apex and running buccally to meet lingual flank of hypoconid. Posthypoeristid descending lingually from hypoconid apex, crossing lingually posterior to buccal crest from entoconid to posterior of entoconid below apex.

M₂ larger and squarer than M₁ with protolophid and hypolophid of about equal length and protoconid and hypoconid in alignment. Similar to M₁ but anterior cingulid longer and broader, precingulid shorter and interlophid valley broader.

M₃ worn in trigonid region but talonid relatively unworn. Crown very similar to M₂ but most structures more clearly defined. Cristid obliqua massive in interlophid region, not much lower than apices of buccal cuspids. Lingual side of interlophid valley more open with greater separation of ventral ends of postmetaeristid and preentocristid. Posthypoeristid sharply defined crossing posterior surface from hypoconid apex to short, almost vertical postentocristid descending from apex of entoconid. Deep, narrow trench between crest of posthypoeristid and buccal crest from entoconid anterior to it.

M₄ unworn. Hypolophid shorter than protolophid. Cristid obliqua originating on anteroheuccal face of hypoconid, below apex. Preentocristid and postmetaeristid separated only by narrow cleft in interlophid valley. Posthypoeristid crest rounded, meeting entoconid much closer to its apex than on anterior molars. Buccal crest from entoconid shorter and less sharply defined.

DESCRIPTION OF PARATYPES.

DENTARY FRAGMENTS. Horizontal ramus not as deep in juveniles as in adults. Posterior mental foramen varies from beneath M₂/M₃. (ho-

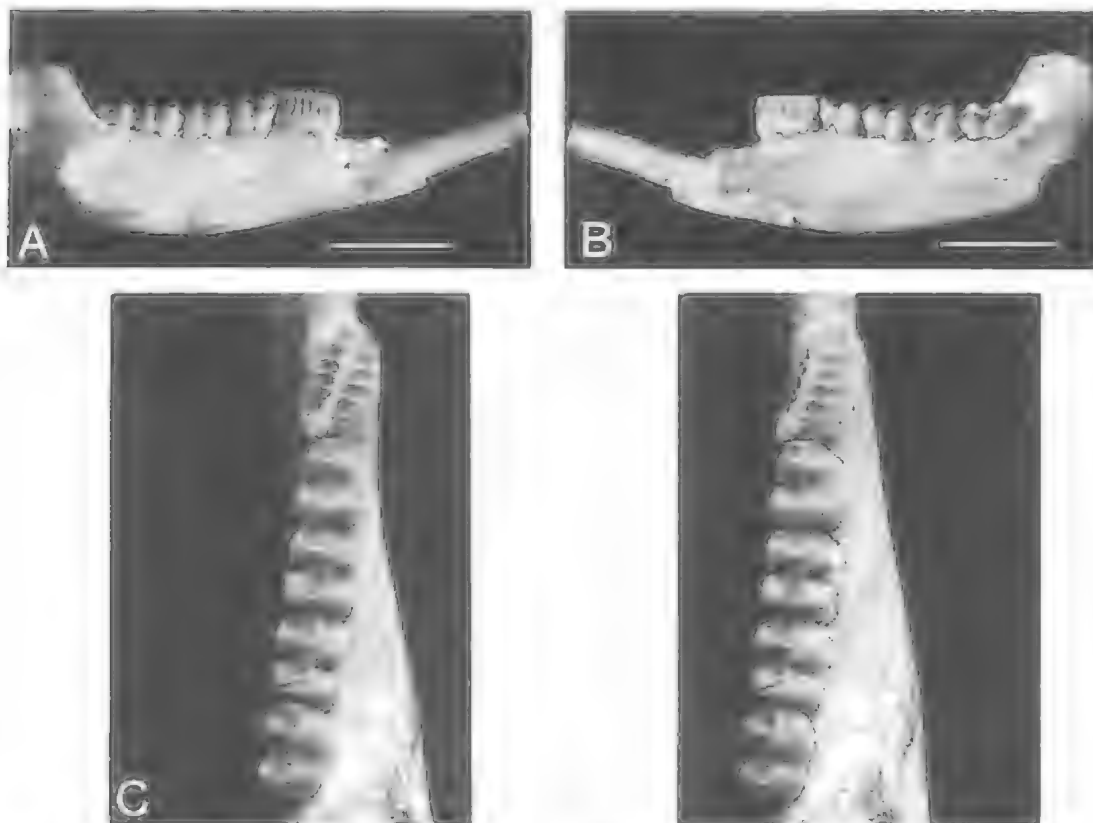


FIG. 1. QMF30390, Holotype, *Nowidgea matrix* sp. nov. A, buccal view; B, lingual view; C, stereopair of occlusal view. Scales = 10mm. AR number is that of the Archer collection, University of New South Wales.

lotype) to as far anterior as beneath hypolophid of M_1 . QMF20080 preserves angular process and much of ascending ramus but lacks condyle and coronoid process. Lingual margin of angular process low, aligned with molar row, posterior margin sloping ventrally towards lingual end. Pterygoid fossa triangular in dorsal view, buccal margin slightly undercutting base of ascending ramus. Mandibular foramen a narrow, vertically oriented ellipse, opening to very short posterior portion of inferior dental canal opening via masseteric foramen to masseteric fossa. Masseteric foramen just visible when masseteric fossa viewed from buccal side. Molar row ventrally concave. Ascending ramus at about 113° to line of a straight edge laid on molar row.

LOWER DENTITION. dP_2 and dP_3 preserved in QMF20080 and 20063, detached dP_3 available for QMF30392. dP_2 (Fig. 2A) short, blade-like, with bulbous base tapering anteriorly and posteriorly. Occlusal margin straight, relatively hori-

zontal, with 4 small cusps anterior to longer, posterior cuspid overhanging posterior base of tooth. Fifth cuspid incompletely differentiated from large, posterior cuspid in QMF20080. Transcristids associated with each of 4 anterior cusps. Posterior, buccal face of crown abutting anterior lingual face of dP_3 .

dP_3 (Fig. 2A) narrower anteriorly than posteriorly, dominated by massive, laterally compressed protoconid, the tallest cuspid on tooth. No distinct metaconid. Paracristid anterolingually directed, descending to paraconid on anterior margin. Cristid descending steeply from paraconid apex to crown base on buccal side of anterior margin. Cristid descending posterior face of protoconid to interlophid valley. Paraconid, paracristid and protoconid form blade-like crest complementing that of dP_2 . Entoconid taller, more angular than hypoconid. Cristid obliqua running anterolingually from apex of hypoconid, crossing interlophid valley and ascending buccal flank of protoconid. In QMF20069 and QMF30392 a short, buccally-



FIG. 2. Paratypes of *Nowidgee matrix* sp. nov. A, stereopair of occlusal view of QMF20080, right dentary fragment with dP2-3, M1-3, (M4). B, stereopair of occlusal view of QMF30395, right maxillary fragment with P3, M1-4. Visible number is that of the Archer collection, University of New South Wales.

directed protostylid crest joining protoconid apex to a prominence (reduced protostylid), contacted by anterior end of cristid obliqua. Sharp pre-entocristid running to interlophid valley from entoconid apex. Buccally-directed crest from entoconid descending steeply buccally from entoconid apex to about midline of tooth. Posthypoconid crest descending lingually from hypoconid apex to shorter postentocristid ascending to entoconid apex.

P3 in QMF19937 and 30394 resembles holotype but with seventh minor cuspid, imperfectly differentiated from long posterior cuspid of occlusal crest. Seventh minor cuspid more clearly differentiated in P3's removed from crypts in QMF20080 and QMF30392.

Except for QMF19961 in which anterior molars very worn, molar teeth in paratypes less worn than those of holotype. Molar morphology among paratypes very similar to holotype.

TABLE 1. Dental parameters for type specimens of *Nowidgee matrix* sp. nov.

Number	P2 l	P2 w	P2 h	P2 tcn	P3 l	P3 w	P3 h	P3 tcn	dP3 l	dP3 aw	dP3 pw	M1 l	M1 aw	M1 pw	M2 l	M2 aw	M2 pw	M3 l	M3 aw	M3 pw	M4 l	M4 aw	M4 pw
F30390					6.0	3.2	3.6	6				3.9	2.8	2.96	4.1	3.1	3.2	4.1	3.2	3.0	4.2	3.1	2.8
F20080	3.9	3.4	3.4	4					3.4	2.2	2.6	3.8	2.4	3.0	4.0	2.5	2.9	3.7	2.6	3.0			
F20069	3.3	2.7	3.0	4	6.4	3.2	3.5	6	3.4	2.0	2.3	3.8	2.7	2.7	4.2	3.1	2.8						
F30391												3.9	2.6	2.8	3.8	3.0	3.0						
F19937					6.4	3.6	4.5	6															
F22761												3.3	1.6	2.0	3.6	2.3	2.3						
F30392									3.4	2.2	2.3	3.6	2.6	2.5	4.2	2.5	2.9	4.2	2.5	2.9			
F19961												4.2	2.5	2.5	4.2	3.1	3.1	3.9	2.8	2.8	3.8	2.7	2.5
F20255																		4.5	3.4	3.1	4.1	3.0	2.8
F19991																		3.9	3.1	3.0	4.1	3.1	
F30393									3.3	2.4	2.5	3.7	2.5	2.5									
F30394					7.1	3.2	3.8	6				4.0	2.2	2.6	3.8	2.9	3.0	4.0	3.1	3.0	4.0	2.9	2.7
MEAN	3.6	3.1	3.2	4	6.5	3.4	3.9	6	3.4	2.2	2.4	3.8	2.4	2.6	4.0	2.8	2.9	3.5	3.0	3.0	4.0	3.0	2.7
SD	.4	.5	.3	0	.5	.3	.5	0	.1	.2	.2	.3	.4	.3	.2	.3	.3	1.5	.3	.1	.2	.2	.1
F30395					7.6	-	3.9	6				4.1	3.8	3.7	4.0	4.2	4.0	4.0	4.1	3.6	3.7	3.4	2.7

2) Maxillary fragment. QMF30395 occludes extremely well with dentary fragment, QMF30394 found in close proximity. Preserves buccal surface of maxilla from diastemal region to masseteric process, including ventral margin of infraorbital foramen, suborbital shelf, alveolar process containing entire cheek tooth row and very narrow portion of palatine wing. Masseteric process of no more than a ventral prominence separated from alveolar process by short, narrow sulcus. Maxillary foramen of infraorbital canal at anterolingual corner of triangular suborbital shelf of maxilla, numerous smaller foramina within ventral margin of foramen. Infraorbital foramen dorsal to midpoint of P³.

UPPER DENTITION. (Fig. 2B). Molar row slightly convex in lateral view, occlusal edge of P³ aligned with buccal margin of molar row which curves slightly lingually anteriorly. Molar size increasing from M¹ to M³; M⁴ markedly smaller than M³.

P³ almost twice length of M¹, lingual margin damaged, buccal margin convex for 2/3 length, becoming concave for remainder. Occlusal margin anteroposteriorly straight, on midline of tooth. Six small cuspules on margin, succeeded by larger, posterior cuspule which has strong lingual ridge associated with its base.

M¹ with straight anterior and buccal margins and convex lingual and posterior margins. Anterior width greater than posterior width but protoloph and metaloph of about equal length. Low crowned with lingual cusps more massive and more rounded than buccal counterparts. Buccal cusps closer to lateral margin of the tooth: buccal surfaces of crown almost vertical, lingual surfaces sloping. Narrow lingual cingulum reaching from anterior, lingual base of protocone to base of metaconule. Protoloph formed by strong paracrista directed lingually from paracone apex and which meets buccal flank of protocone below apex. Preparacrista runs anteriorly from paracone apex to anterior margin and is continuous with anterior margin of paracingulum bounded laterally by preparacrista and anterobuccally inclined preprotocrista which meets anterior margin anterior to junction of paracrista with protocone. Very large stylar cusp C closing interloph valley on buccal side. Postparacrista and premetacrista reaching floor of interloph valley from respective cusp apices, but not united. Postprotocrista strongly developed but worn in interloph region, contacting metaloph crest just buccal to apex of metaconule. Prominent neometaconule at about centre of metaloph with rounded crista running posteriorly for about half height of metaloph. Postmetaconule crista buccally inclined on pos-

terior face of metaconule, crossing posterior base of metaloph as margin of strong metacingulum, contacting posteriorly directed postmetacrista at base of metacone.

M² considerably wider anteriorly than posteriorly, occlusal outline more bluntly triangular. Crown differing from M¹ in: lingual cingulum continuous with precingulum extending anteriorly across base of protocone to anterior end of preprotoecrista; styler cusp C slightly more anteriorly positioned on buccal flank of paracone and does not completely close buccal end of interloph valley; neometaconule and its crista less obvious. M³ very similar to M² but lingual cingulum not as sharply defined, styler cusp C smaller, postparaecrista and premetacrista unite to form continuous centroecrista. M³ much smaller than anterior molars. Metaloph markedly shorter than protoloph. Lingual cingulum separated from precingulum, all cristae sharply defined. Metaconule lower; no neometaconule or styler cusp C.

REMARKS. *Nowidgee matrix* is similar in size to *Bulungamaya delicata* but has bunolophodont, rather than lophodont molars. Its bunolophodont lower molars resemble those of *Purtia mosaicus*, but molar occlusal outline in *N. matrix* is more rectangular, rather than square as in *P. mosaicus*. P₃ of *N. matrix* differs from that of *P. mosaicus* in having 6-7 rather than 8 transcrisids and, while having a bulbous base, lacks the distinct lateral cingulids of *P. mosaicus*. It differs from *P. mosaicus* in having an I₁ which has both ventral and dorsal enamel flanges and in having enamel which, while confined to the buccal surface, extends over that surface rather than being confined to its ventral portion as in *P. mosaicus* and other potoroines. Lower molars of *N. matrix* are similar to lower molars from the Tarkarooloo Local Fauna assigned by Flannery and Rich (1986) to *Gumardee*, but differ from them by being smaller in size. P₃ of *N. matrix* has 6-7 transcrisids, apparently many fewer than the P₃ from the Tarkarooloo *Gumardee*, in which the posterior half, the only portion recovered, has 6 transcrisids.

Among potoroines a dorsal enamel flange on I₁ is confined to *Hypsiprinnodon*, *Potorous*, bulungamayines (Flannery et al., 1984) and *Milliyowi bungandij* (Flannery et al., 1992). *N. matrix* differs from *Hypsiprinnodon* by having permanent premolars which are elongated with horizontal or concave occlusal margins rather than plagiolacoid with convex occlusal margins, by failure to retain dP₂ after the eruption of P₁ and by having less disparity between the lengths of

protolophid and hypolophid on M₁. *N. matrix* differs from *Potorous* by having lower molars in which the buccal cusps are positioned lingual to the adjacent lateral margin with the result that buccal crown walls are not as steep as in *Potorous*. *N. matrix* differs from the similarly strongly bunolophodont early Pliocene *Milliyowi bungandij* in having a strongly developed styler cusp C on M¹ (absent in *M. bungandij*) and in lacking branches of the transcrisids of P₃.

The resemblance of the I₁ dorsal enamel flange to that of macropodids is suggestive of a similarly macropodid-like cutting action during occlusion of upper and lower incisors, an unusual feature in an animal with bunolophodont molars similar to those of omnivorous potoroines in which incisors perform a more forecupulate function.

The posteroventrally inclined buccinator sulcus in *N. matrix* was termed the 'labial groove' by Storton (1963) who noted it in *Protemnodon* and other macropodids. Woodburne (1967) reported a similar structure in *Hadronomus puekridgi*. Where such a sulcus occurs among macropodids and other potoroines it is usually closer to and parallels the alveolar margin.

The reduced cuspid on the buccal flank of the large, central cuspid of the dP₃ trigonid which is linked by ridges to the apex of that cuspid and to the cristid obliqua, is interpreted herein as a reduced protostylid since it occurs in the corresponding position and bears the same relationship to the cristid obliqua as do similar structures on M₁ of other species, i.e., the protostylid crest of *Wururoo dayamayi* Cooke, this volume, the discrete protostylid of *Nambaroo saltavus* Flannery & Rich, 1986, and the protostylid of *Palaeopotorous priscus*. The dominant trigonid cuspid lingually adjacent to the protostylid on dP₃ of *N. matrix* and from which the paraecristid arises is thus the protoconid and the metaconid has been lost. The loss of the metaconid of dP₃ may be, as suggested by Ride (1993), the result of a need to supplement the shearing crest of dP₂ which is shorter than the permanent premolar in this species.

Apart from the discrete protostylid rather than a protostylar ridge, the holotype tooth of *P. priscus*, designated as M₁ (their M₂) by Flannery & Rich (1986), bears strong similarities to dP₃ in paratypes of *N. matrix*. Undescribed Riversleigh bulungamayines also have a protostylar ridge on dP₃ and a posterobuccally inclined protolophid similar to *P. priscus*. Since the latter character does not occur on molar teeth of plesiomorphic species such as *N. matrix* which have otherwise

similar bunolophodont molars, it is suggested that the holotype tooth of *P. priscus* is dP₃ rather than M₁. If this is the case, *P. priscus* must still be regarded as more plesiomorphic than *N. matrix* in view of the discrete protostylid on this tooth, but other differences in this tooth, or in molars referred to this species, are here regarded as insufficient to warrant the erection of a new subfamily. Subfamilial affinities of the species remain uncertain: its bunolophodont molar morphology suggests it may represent either a plesiomorphic potoroine or bulungamayine. However, the discrete protostylid on the holotype (dP₃) is plesiomorphic and the species may prove to be basal to both these taxa.

Lower molars in *N. matrix* are suitable to be ancestral to *B. delicata*. Lophids in *N. matrix* are clearly formed by transverse cristids extending buccally from the lingual cuspids. The posterior cingulid is enclosed by the posthypocristid which sweeps lingually posterior to the hypolophid and low on the crown before linking to the postentoconid on the posterior of the entoconid. In *B. delicata* the protolophid is formed in a manner similar to that of *N. matrix* but joins the protoconid closer to its apex. The posthypocristid is more elevated on the crown, more transversely oriented and links to the entoconid much closer to the entoconid apex. The buccally oriented crest from the entoconid is reduced in length and in prominence, the posthypocristid having formed a neomorphic hypolophid.

In the low-crowned upper molars of *N. matrix*, lophids are formed by cristae extending lingually from the buccal cusps, upper and lower molars showing reversed symmetry in this respect. Longitudinal crests, notably the pre- and postproto-crista are emphasised, as they are in *Gumardee pascuali*. Strong longitudinal cristae characterise bunolophodont upper molars as defined by Flannery et al. (1984) who suggested that these might work in a different way to lophodont molars in which transverse rather than longitudinal cutting crests are emphasised.

In some undescribed plesiomorphic Riversleigh balbarines (pers. obs.) stylar cusps C and D or their stylar crests are present in the interloph region. *N. matrix* retains only stylar cusp C and lacks any trace of stylar cusp D. While both balbarines and bulungamayines are likely to be derived from bunolophodont ancestors, the absence of stylar cusps other than C in what is an extremely plesiomorphic bulungamayine, suggests that loss of other stylar cusps had already occurred in the bulungamayine ancestor which

must in this aspect at least, be more derived than that of balbarines.

Ganguroo gen. nov.

TYPE SPECIES. *Ganguroo bilamina* sp. nov.

DIAGNOSIS. Bulungamayines with lower molars which are completely bilophodont, lacking any trace of a buccally-directed crest originating from the entoconid and anterior to the hypolophid.

REMARKS. *Ganguroo* gen. nov. differs from all potoroines, hypsiprimnodontines and propleopines by having bilophodont lower molars. It differs from all macropodines and sthenurines by having a combination of: low-crowned molars; finely-ridged, elongate premolars; a deeply penetrating masseteric canal confluent over its length with the inferior dental canal. It differs from all balbarines by having the elongate, finely-ridged premolars referred to above, lacking a transversely compressed trigonid on M₁ and in lacking a posterior cingulid on lower molars.

ETYMOLOGY. Waanyi (as spoken by Ivy Stinken, formerly of Riversleigh Station) *gangu*, grandfather and 'roo' is a common Australian diminutive for kangaroo.

Ganguroo bilamina sp. nov. (Fig. 3, Table2)

DIAGNOSIS. As for the genus

MATERIAL EXAMINED. Holotype QMF19915 from Wayne's Wok, Hal's Hill' D-Site Plateau. Paratypes QMF19591, 18810, 19814, 19835, 30398, 30399 from Wayne's Wok Site; QMF19868, 19870, 19966, 30400 from Camel Sputum Site, Godthelp's Hill; QMF19642, 20293, 30396, 30397 from Upper Site, Godthelp's Hill; QMF19988 from Mike's Menagerie Site, Godthelp's Hill; QMF23777 from Bites Antennary Site, eastern part of D Site Plateau. All System B, Miocene sites (Archer et al., 1989).

ETYMOLOGY. Latin *lamina*, blade; refers to the bilophodont lower molars.

DESCRIPTION OF HOLOTYPE. Left dentary including horizontal ramus, most of angular process and part of ascending ramus. I₁, P₃ and M₁₋₄ preserved. Ventral margin of horizontal ramus strongly convex, deepest below protolophid of M₃, distinct digastric prominence on the ventral margin at this point. Diastema relatively short, less than 20% of length of cheek tooth row. Slender I₁ almost horizontal with dorsal occlusal

margin well below plane of cheek tooth row. Alveolus for very small I₂ on dorsal margin of diastema just posterior to margin of I₁ alveolus. Mental foramen close to dorsal margin of diastema below anterior margin of P₃. 2 very small posterior mental foramina more posteriorly, 1 below hypolophid of M₂, the other below protolophid of M₃. Very shallow sulcus for attachment of buccinator muscle sloping diagonally ventrally on buccal surface below M₁-M₂. Ascending ramus at about 105° to line of a straight edge laid across high points of occlusal surfaces of cheek tooth row. Since tooth row concave dorsally, such a line contacts posterior of P₃ and hypolophid of M₄. Buccal margin of masseteric fossa straight with flat area for attachment of parts of superficial layer of masseter extending anteroventrally. Masseteric canal and inferior dental canal confluent anterior to large masseteric foramen. Diameter of foramen and anterior constriction of common canal suggest insertion of deep layer of masseter unlikely to have reached much more anteriorly than M₃. Posterior to masseteric foramen inferior dental canal very short; masseteric foramen almost overlapped by mandibular foramen. Lingual margin of angular process aligned with molar row. Wide, shallow basin of pterygoid fossa overhanging buccally by remaining anterior portion of ascending ramus. Mandibular symphysis decreases in height posteriorly, extends to level of posterior margin of P₃.

Dentition. Cheek tooth row anteroposteriorly straight; P₃ flexed slightly buccally out of alignment. In lateral view occlusal margin of P₃ above that of molars. Molars low crowned, bilophodont, no trace of any buccally-directed crest associated with the entoconid. Molar size increases from M₁ to M₃; M₄ is smaller than M₃.

I₁ long and slender with low dorsal and ventral enamel flanges. Dorsal and ventral margins almost horizontal for most of length before latter converges on former at anterior end. Enamel confined to buccal surface. Cross section circular close to alveolar margin, triangular anteriorly, resulting from development of rounded, longitudinal ridge central to lingual surface.

P₃ elongate, blade-like with mostly horizontal occlusal margin serrated over most of length anterior to large, posterior cuspid taller than rest of tooth. Serrations formed by 6 minor cuspids, each with associated transcrisids, most posterior of these least distinct and shortest. In occlusal view crown base tapering anteriorly and posteriorly to rounded margins. Buccal margin convex, lingual margin relatively straight. Lingual base of crown

bulbous adjacent to central region of occlusal blade, forming poorly-defined, rounded lingual cingulid. Occlusal margin following midline but posterior cuspid flexed lingually. Cristid descending anteriorly from apex of most anterior cuspid to crown base and posterior margin delineated by similar but shorter cristid descending from posterior cuspid.

M₁ subrectangular in occlusal outline, narrower anteriorly than posteriorly. Lingual walls of crown subvertical, buccal side sloping more gently. Tooth worn, more wear on buccal side. Wear facet on posterior of metaconid and breaches in enamel of protoconid, hypoconid and entoconid. Metaconid taller, more angular than protoconid which has been reduced in height by wear. Sharply defined crest of protolophid descending buccally from apex of metaconid to that of protoconid. Short paraeristid running anteriorly from base of protoconid to anterior margin. Steeply descending enamel ridge on anterior margin buccal to paraeristid, forming margin of short precingulid. Broad anterior cingulid enclosed between paraeristid and premetaeristid which runs between metaconid apex and anterior margin. Sharp postmetaeristid descending posteriorly from metaconid apex to interlophid valley, meeting similarly well-defined preentocrisid running anteriorly from apex of the entoconid. Cristid obliqua worn, running anterolingually on anterior face of hypoconid before turning anteriorly across interlophid valley, meeting posterior face of protolophid lingually adjacent to protoconid base. Entoconid taller than hypoconid which is more worn. Crest of hypolophid crossing from posterior of hypoconid apex to meet entoconid apex centrally. Postentocrisid descending posterior face of entoconid but no other ornamentation of posterior face of hypolophid. M₂ similar in outline to M₁ but slightly larger and less worn. Metaconid taller than protoconid but hypoconid and entoconid subequal in height. Postmetaeristid and preentocrisid not uniting in interlophid valley. M₃ largest of molars, unworn, with all cuspids about equal height; lingual cuspids with more angular apices than buccal cuspids. M₁ damaged, lacking protoconid and most of anterior margin. Hypoconid taller than entoconid; no postentocrisid.

DESCRIPTION OF PARATYPES. Condyle preserved in QMF19814, 19870, 19810 and 30396. In QMF19870 and 19814 is transversely elongate with rounded posterior margin. In QMF30396 condyle has more circular outline. That of

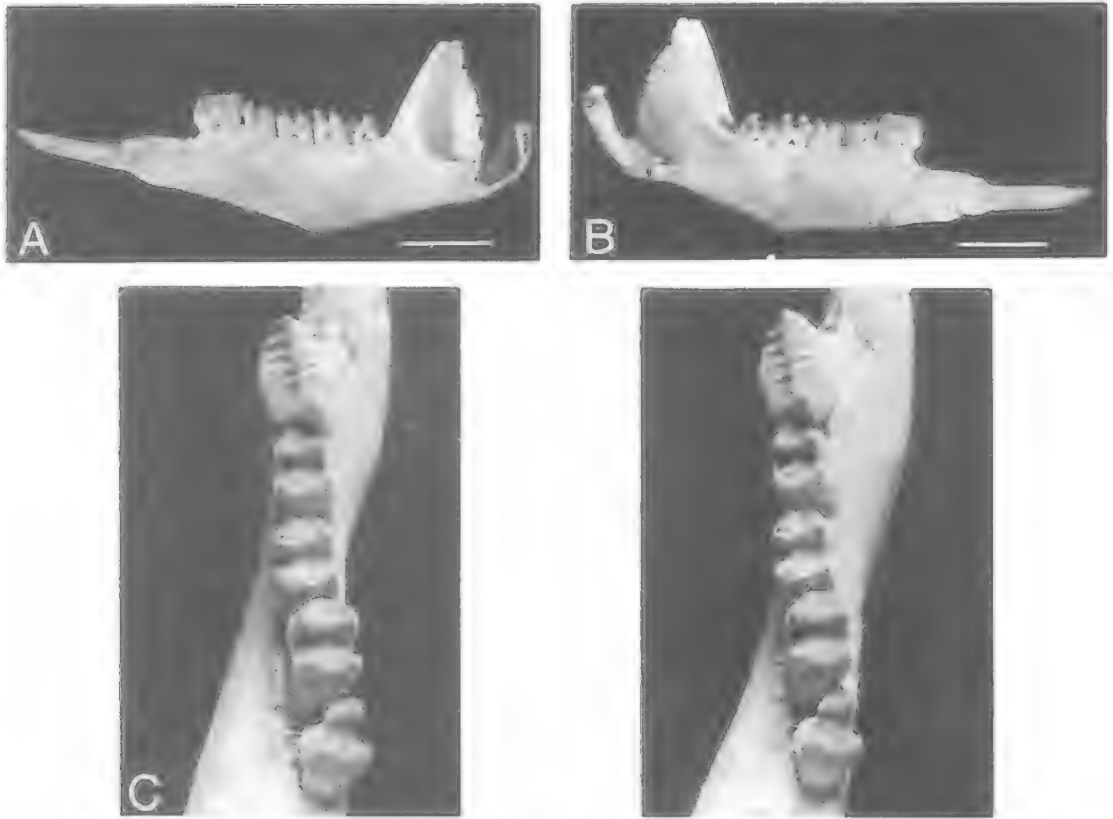


FIG. 3. QMF19915, Holotype of *Ganguroo bilamina* sp. nov. A, buccal view; B, lingual view; C, stereopair of occlusal view. Scales = 10mm.

QMF19810 slightly damaged lingually but similar to, although somewhat smaller than, that of QMF19870 and QMF19814. Differences in shape possibly age related since QMF30396 is from a subadult animal, indicated by incompletely erupted P₃. Height of condyle above plane of molar row varies from 7mm in QMF19870 and QMF30396 to 11mm in QMF19810, variation possibly being size related. Angle of ascending ramus relative to plane of molar row varies 120° (AR12517)–108° (QMF18814).

Digastric process on ventral margin of horizontal ramus apparently variable within species: QMF19814 level of development comparable to that of holotype, but other paratypes show lesser or no such development. Number of posterior mental foramina also variable: most paratypes have only one such foramen, consistently located below M₂, but none present in QMF30398 while two present in QMF30400 and QMF19966. QMF19988 has number of smaller foramina accessory to mandibular foramen and also has sul-

cus for vessels of inferior dental canal on lingual wall of masseteric fossa. Posterior portion of inferior dental canal between masseteric foramen and mandibular foramen longer in AR12517 than in holotype and most other paratypes. QMF30400 and QMF19988 have direct opening via single foramen from pterygoid fossa into masseteric fossa with no intervening canal (the condition usual among extant macropodoids).

Damage to ventral margin of horizontal ramus reveals extent of anterior insertion of masseter, in QMF19868 and QMF20293 it reaches level of M₂ hypolophid, but only to level of M₃ hypolophid in QMF30397.

DENTITION. dP₂ and dP₃ in QMF19835, 23777. dP₂ small, blade-like with rounded anterior and posterior margins, strongly convex buccal margin and straight lingual margin. Occlusal crest serrated over much of length anterior to large posterior cuspid overhanging posterior base of crown. QMF19835 has 3 small cuspids in serrated region, each with associated transcrisids; 4

TABLE 2. Dental parameters for type specimens of *Ganguroo bilamina* sp. nov.

Number	I ₁ l	I ₁ w	P ₂ l	P ₂ mw	P ₂ h	P ₂ tcn	P ₃ l	P ₃ mw	P ₃ h	P ₃ tcn	dP ₃ l	dP ₃ aw	dP ₃ pw	M ₁ l	M ₁ aw	M ₁ pw	M ₂ l	M ₂ aw	M ₂ pw	M ₃ l	M ₃ aw	M ₃ pw	M ₄ l	M ₄ aw	M ₄ pw	
F19915	11.6	2.2					5.9	3.3	3.9	6				3.7	2.4	2.6	3.7	2.7	2.8	3.7	2.6	2.6	3.8	-	2.6	
F30400																		3.9	2.8	2.9	3.7	2.8	2.8	3.8	2.8	2.7
F23777			4.2	2.5	3.1	3					3.5	2.0	3.3	3.6	2.8	3.0										
F19868	10.9	2.1					5.9	3.1	3.7	5								3.8	2.9	2.8	3.8	2.9	2.9			
F19870											4.2	2.6	2.8	4.0	2.8	3.0	3.8	3.1	3.1	4.0	2.9	2.8				
F19966							5.9	3.1	3.9	6	3.4	2.6	2.8	3.8	2.8	3.0	3.9	3.1	2.9	3.9	3.0	2.7				
F19988																				2.8	3.8	2.8	2.8	3.6	2.9	2.5
F30396		1.7					5.3	2.4		6				3.4	2.6	2.6	3.7	2.7	2.7	3.9	2.9	2.7				
F30397							6.3	3.1	3.7	7				3.5	2.3	2.5	3.9	2.7	2.8	3.9	2.9	2.8	3.9	2.7	2.5	
F19642							5.6	2.3	3.9	6				3.5	2.1	2.4										
F20293																		4.1	3.0	3.0	3.9	3.0	2.9	3.9	2.9	2.9
F30399							6.2	2.8	3.6	7				3.5	2.2	2.7	3.5	2.5	2.9	3.6	2.7	2.8	3.8	2.7	2.7	
F30398							6.1	3.0	3.5	6				3.5	2.6	2.7	3.6	3.0	2.9	3.8	3.0	2.8	3.5	2.8	2.3	
F19591																					3.9	3.2	2.7			
F19810														3.6	2.6	2.6	3.8	2.8	2.8	3.8	2.7	2.9	3.7	2.8	-	
F19814							5.9	3.2	3.7	6				3.6	2.5	2.8	3.7	2.6	3.0							
F19835			3.4	3.0	3.6	4	5.7	2.8	4.0	5	2.9	2.3	2.3	3.1	2.5	2.7										
MEAN	11.3	2.0	3.8	2.8	3.4	3.5	5.9	2.9	3.8	6	3.5	2.4	2.8	3.6	2.6	2.7	3.7	2.9	2.9	3.8	3.0	2.8	3.7	2.9	2.6	
SD	4.9	.3	.6	.4	.4	.7	.3	.3	.2	.7	.5	.3	.4	.2	.4	.2	.4	.3	.1	.3	.3	.1	.3	.4	.2	

such cuspids in QMF23777. Anterior and posterior margins of crown delineated by vertical cristids descending from ends of occlusal crest. Occlusal crest runs slightly lingual to midline, lingual surface of crown more steeply inclined than buccal.

dP₃ better preserved in QMF23777 and used as basis for description below. Crown base roughly rectangular in occlusal outline, narrowing somewhat anteriorly. Protolophid extremely laterally compressed, inclined posterolingually, dominated by tall protoconid with thick, rounded protostylid crest descending its buccal flank. Metaconid cannot be distinguished from protoconid. Prominent paracristid (less so in QMF19835) runs anteriorly to tall paraconid (shorter in QMF19385) on anterior margin. Paraconid, paracristid and protolophid form blade-like crest complementing that of dP₂. Vertical cristid descends from posterior margin of protolophid crest to interlophid valley and is contacted by anteriorly directed preentocristid in QMF19835, but not in this specimen. Hypolophid transversely oriented, concave in posterior view. Cristid obliqua runs anterolingually on anterior face of hypoconid, turning anteriorly across interlophid valley and contacting protostylid crest. No ornamentation on posterior face of hypolophid.

P₃ in most paratypes closely resembles that of holotype but QMF30399 has 7 minor cuspids rather than 6.

Molar morphology very similar to that of the holotype although variable postentocristid between different specimens and between different teeth in single specimens.

DISCUSSION

The horizontal orientation of I₁ is similar to that in macropodines in which there is considerable ventral flexion of the rostrum, necessary to bring upper and lower incisors into occlusion and there would presumably be a corresponding flexion of the rostrum in this species. dP₃ is very similar to that of *N. matrix* but is more derived in that the reduced protostylid of *N. matrix* is here further reduced to a protostylid crest. Molars in this species are more derived than in either *N. matrix*, *B. delicata* or *Wabularoo naughtoni* because they are lophodont.

N. matrix, *B. delicata* and *G. bilamina* represent stages in an evolutionary sequence in which a bunolophodont, omnivorous ancestral form is changed to that of a lophodont herbivore (Fig. 4). Hypolophid morphology is particularly informative in this respect. As discussed earlier, a neomorphic hypolophid has been developed in *B. delicata* by elevation of the posthypocristid on

the crown and directing the posthypocristid more transversely. Hypolophid morphology in *W. naughtoni* closely resembles that of *B. delicata*. The bunolophodont origin of this morphology is indicated by the reduced buccal crest from the entoconid anterior to the new hypolophid, representing the remnant of the original hypolophid crest. No trace of this crest is evident in *G. bilamina*, the neomorphic hypolophid crest being formed entirely by the elevated, transverse posthypocristid as indicated by the presence of a postentocristid on the posterior face of the entoconid. Loss of the buccally-directed crest from the entoconid represents a subtle change in morphology between *N. matrix* and *G. bilamina* but a highly significant apomorphy.

The evolutionary series represented by these bulungamayine taxa demonstrates that lophodonty evolved independently twice among Oligocene-Miocene kangaroos - once in balbarines in a process which seems to have been essentially that proposed by Flannery & Rich (1986) and once among bulungamayines using the mechanism proposed above. While Flannery (1989) suggested that balbarines were ancestral to macropodines and sthenurines, the similarity of premolar and molar morphology of derived bulungamayines such as *G. bilamina* to that of the later Miocene macropodids from Alcoota is greater than that of more derived balbarines such as *Balbaroo* in which on M_1 there is still considerable lateral compression of the protolophid and little development of the anterior cingulid. The premolar of balbarines is also much shorter than that of bulungamayines and the plesiomorphic Alcoota macropodids (Cooke, 1997).

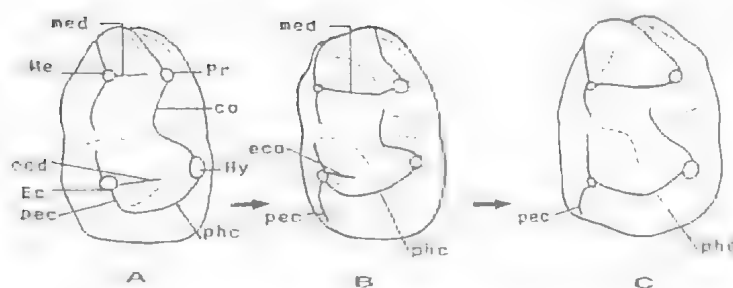
Lower molar morphology of *G. bilamina* has strong similarities to that of the much larger *Hadronomus puckridgi* Woodburne, 1967 from Alcoota which Murray (1991) regarded as a plesiomorphic sthenurine. Both species are low-crowned and bilophodont, have long anterior cingulids, have M_1 protolophids which are not laterally compressed and lack posterior cingulids, although *Hadronomus* has a bulbous base to the hypolophid. *Hadronomus* also has an elongate premolar, resembling in that respect the premolar of bulungamayines, but that of *Hadronomus* is more coarsely serrated than that in any of the known bulungamayine species and bears well developed lingual and buccal cingula, not present in bulungamayines. However, paratypes of *N. matrix* show variable differentiation of minor cusps and transcrists on P_3 , indicating some lability in degree of serration of the occlusal

margin of this tooth in bulungamayines. The bulbous base of the bulungamayine P_3 could serve as an adequate precursor of lateral cingula (a lingual cingulum is poorly developed on P_3 of *G. bilamina*). The premolar of all known balbarines is in contrast a shorter, more plagiaulacoid tooth.

Similarities also exist between dental morphology in *G. bilamina* and in *Dorcopsoides fossilis*, also from Alcoota. While this species was originally included within Potoroidae, Bartholomai (1978) placed it in Macropodinae. Both species have elongate premolars. Lateral cingula are lacking in P_3 of *Dorcopsoides* while a lingual cingulum is poorly developed in that of *G. bilamina* and there are again differences in serration and transcrists between the two species.

dP_3 in *N. matrix* and *B. bilamina* has some similarity with that of *Dorcopsoides* in that the metaconid is reduced or absent in each. Woodburne (1967) also noted the 'fused protoconid and metaconid' of dP_3 in *Dorcopsoides* and 'a short posterolabial crest ... which turns abruptly posteriorly before descending into the transverse valley and continues posterolabially up the anterior face of the hypoconid'. This crest may be homologous with the protostylid crest which is linked to the cristid obliqua of dP_3 in *N. matrix* and *G. bilamina* but which is also present on dP_3 in undescribed Riversleigh balbarines referable to *Nambaroo* and in which there is also considerable abbreviation of the protolophid (pers. obs.). Ride (1971) suggested that close proximity of the protoconid and metaconid on dP_3 is plesiomorphic for macropodoids (his macropodids), and the protostylid or its reduced form of a protostylid crest in both potoroids and macropodids suggests that this character is similarly plesiomorphic.

While lower molar morphologies in *G. bilamina* and *Dorcopsoides* are similar in many respects, they differ markedly in that *Dorcopsoides* has a well-developed posterior cingulid, absent in all bulungamayines but present in balbarines. Derivation of *Dorcopsoides* from a bulungamayine ancestor would require development of a neomorphic posterior cingulid, such development possibly indicated by the swollen hypolophid base of *Hadronomus*. Evolution from a balbarine ancestor would require modification to both the anterior cingulid and compressed protolophid of M_1 , but modification of pre-existing structures is a more usual evolutionary phenomenon than the development of new structures. This notwithstanding, dental morphology in bulungamayines is such that, on



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FIG. 4. Development of lophodonty in bulungamayines, illustrated by RMJ. A, *Nowidgee matrix*. B, equivalent to *B. delicata*. C, *G. bilamina*. Abbreviations: Pr=protoconid, Me=metaconid, med=metacristid, HY=hypoconid, Ec=entoconid, ecd=buccal crest from entoconid, phc=posthypoconid, pec=postentocristid, co=cristid obliqua.

the grounds of parsimony, they, rather than balbarines, must be preferred as the group most closely ancestral to macropodids.

In the hypothesis of molar evolution within Bulungamayinae advanced herein, there is a transition from a potoroid-like molar in basal species to a macropodid-like molar in derived species. Such a transitional sequence within the group may explain the differing views of familial affinity of bulungamayines (Case, 1984; Woodburne, 1984; Flannery et al., 1984). At the time their respective views were advanced, only 2 bulungamayine species, *B. delicata* and *W. naughtoni*, had been described. Molar morphology in both those species is intermediate in the transitional sequence and it is not surprising that both macropodid and potoroid affinities could be argued on the basis of these species.

If, as seems likely from the evidence provided herein, that bulungamayines are directly ancestral to macropodids, then monophyly of Bulungamayinae cannot be stated with certainty. Further doubts also arise concerning monophyly of Macropodidae.

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BIOSTRATIGRAPHIC IMPLICATIONS OF FOSSIL KANGAROOS AT RIVERSLEIGH, NORTHWESTERN QUEENSLAND

B.N. COOKE

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Kangaroos form an important component of the faunal assemblages of Riversleigh and most other Australian Cainozoic fossil deposits. Attempts to use fossil kangaroos to determine the relative ages of Riversleigh sites suggests that overall faunal composition may be a more useful guide to relative age than presence or absence of particular species. Marked changes in kangaroo faunal composition occur between Riversleigh System B and C sites with the apparent extinction of most balbarine species and rise to dominance by lophodont bulungamayine species. This change correlates with climatic decline following mid-Miocene climatic optima. Approximate age equivalence is suggested between Riversleigh System B sites and faunal zones B + C (Woodburne et al., 1993) of the Etadunna Formation, South Australia. Riversleigh's System A sites are older. The more derived, lophodont bulungamayines of Riversleigh System C are considered potentially ancestral to plesiomorphic macropodids such as *Hadronomas* from the Alcoota Formation. Kangaroos support an age span for pre-Pliocene deposits at Riversleigh that extend from the late Oligocene to late middle Miocene and possibly early late Miocene. □ *Kangaroos, Oligocene, Miocene, Pliocene, Riversleigh.*

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Tedford (1967) provided the first description of kangaroos from Riversleigh. Since then the area has yielded many thousands of kangaroo fossils representing at least 32 new species.

Archer (1979) described *Wabularoo naughtoni* from D Site. Flannery et al. (1982) described *Bulungamaya delicata* (erecting the Bulungamayinae), *W. naughtoni*, *Balbaroo gregoriensis* from Riversleigh, *B. camfieldensis* from Bullock Creek, Northern Territory (middle to Late Miocene) and a single specimen of *Balbaroo* from Kangaroo Well. The species of *Balbaroo* were placed in a new macropodid Balbarinae. They also described the potorine *Gumardee pascuali* and macropodid *Galanarla tessellata* from Riversleigh.

Archer & Flannery (1985) described the Riversleigh propleopine *Ekaluteta ima*. Flannery & Archer (1987a) described *Hypsiprymnodon bartholomaei* and (1987b) *Bettongia moysesii*, the only pre-Pliocene representatives of these genera. Cooke (1992) described the balbarine *Ganawamaya* with *G. acris*, *G. aediculus* and *G. ornata*.

The number of Riversleigh fossil kangaroo specimens, ranging from isolated teeth, isolated postcranial elements, maxillary and dentary fragments to complete skulls is almost overwhelming. I have concentrated on the more complete

remains available. These indicate a further 21 new species, a number of which are described in this volume. *Protemnodon* sp. has been recorded from the Pliocene Rackham's Roost Site and *Macropus agilis* has been recorded from the Pleistocene Terrace Site (M. Archer pers. com.).

This brings the total Riversleigh macropodoid fauna to 34, including the Potoroinae, Hypsiprymnodontinae, Propleopinae, Balbarinae, Bulungamayinae and Macropodinae.

Archer et al. (1989) recognised more than 100 local faunas from the Riversleigh fossil area, with ages estimated to range from Oligocene-Miocene to Holocene. (Discoveries since 1989 have raised that number to more than 150 sites with faunal assemblages). They grouped the Oligocene-Miocene sites into three 'Systems' designated A-C, with System A sites regarded as oldest and System C sites as youngest.

Megirian (1992) treated the entire sequence of fossiliferous Limestone overlying the Thornton Limestone as comprising the Carl Creek Limestone. He used the 'Systems' of Archer et al. (1989) in a purely biostratigraphic sense and has later (1994) challenged the use of the System concept on the grounds that the terminology has been unsatisfactorily defined and that there is no precedent for such usage in lithostratigraphic nomenclature.

TABLE 1. Sites of occurrence and numbers of specimens of each identified pre-Pliocene Riversleigh macropodoid species. QL=Quantum Leap; WH=White Hunter; DU=Dunsinane; COA=Cleft of Ages; BA=Bitesantennary; DT=Dirk's Towers; OUT=Outasite; WW=Wayne's Wok; BO=Boid; CS=Camel Sputum; IN=Inabeyance; MM=Mike's Menagerie; UP=Upper; CR=Creaser's Ramparts; N'sG=Neville's Garden; LM=Last Minute; FF=Firestone Favourites; H'sH=Henk's Hollow; TT=Two Trees; DO=Dome; J'sC=Jim's Carousel; ENC=Encore; ?=uncertain position within the System sequence of Archer et al. (1989).

SPECIES	Syst. A		? A/B						Syst. B										?B	Syst. C					?mid Mio	Uncert			
	D	G	Q L	W H	D U	C O A	B A	D T	Lower			Higher								intr.	Low C	Mid C	Higher C	?					
									R S O	U T	W	B O	C S	I N	M	U P	C R												
gen.Wan. sp.1																				2							1		1
gen.Wan. sp.2																					1	1			3				1
Bu.delicata	1	1	1																	3									
Wab. naughtoni	1																			5									
Gan. bilamina																													
Gan. sp.2																													
Bel. moyesii																													
E. ima																					1								
H. bartholomai																					1								
Gum. pascuali																													
Now. matrx																													
Now. sp.2																													
Bal. gregonensis																													
Bal. sp.2																													
Bal. sp.3																													
Bal. sp.4																													
Gal. tessellata																													
Gan. acris																													
Gan. aediculis																													
Gan. ornata																													
Gan. sp.4																													
Wur. dayamayi																													
Wur. sp.2																													
Wur. sp.3																													
Nam. couperi																													
Nam. sp.2																													
Nam. sp.3																													
Nam. sp.4																													
Nam. sp.5																													
Nam. sp.6																													
Nam. sp.7																													
Nam. sp.8																													

Archer et al. (1989) Archer, Hand and Godthelp (1991) and Archer et al. (1994) interpreted the older Riversleigh local faunas, those from sites in Systems A-C, as representing rainforest communities. This interpretation was made on the basis of characteristics of those faunas such as: high species diversity; presence of complex feeding guilds of small, sympatric mammals; high numbers of obligate leaf eaters in single local faunas, indicating high tree species diversity; presence of high numbers of known rainforest taxa; high numbers of browsing marsupials but absence of grazers.

Megirian (1992) disputed the hypothesis of a rainforest palaeohabitat for the older Riversleigh local faunas on the grounds of his interpretations of drier, even semi-arid environmental conditions prevailing during the genesis of the fossiliferous limestones. He suggested instead that the high species diversity evident in the local faunas resulted from a combination of resident rainforest communities inhabiting rainforest refugia confined to permanent water bodies, and the use of

such permanent water by animals drawn from more distant, mesically adapted communities.

None of the Pre-Pliocene kangaroos from Riversleigh exhibit dental adaptation for a grazing habit which might be expected if they were drawn from a more arid environment. Regardless of their palaeohabitat, kangaroos have a widespread occurrence and are abundant among the many local faunas now known from Riversleigh. They should prove to be important in attempts to determine relative ages of those assemblages. This paper presents the results of a preliminary attempt to use kangaroo fossils to assess relative ages of sites within Riversleigh, assess the age of Riversleigh deposits relative to those of other Australian Tertiary sites which have yielded comparable kangaroo fossils, and to correlate changes apparent within the macropodoid fauna of Riversleigh with Tertiary climatic and geologic events. As part of that attempt, the Systems concept of Archer et al. (1989) has been used as an hypothesis which can be tested using the dis-

tribution of fossil kangaroo species in sites previously assigned to each of systems A, B and C.

INTER-SYSTEM COMPARISONS AND OTHER RELATIONSHIPS AT RIVERSLEIGH

Pre-Pliocene Riversleigh sites that have yielded identified macropodoid species, together with the number of specimens of each, are shown in Table 1.

Column headings in this Table follow Archer et al. (1994) who listed sites known to that date, indicating those confidently assigned to Systems A-C, provided indications of possible System affinities of some sites, and estimated ages of other sites whose faunal composition differs from those allocated to these Systems. As indicated in Table 1 and discussed further below, evidence drawn from the distribution of kangaroo fossils is not in complete agreement with ages suggested by Archer et al. (1994) for some Riversleigh sites. Site G of Flannery et al. (1982) is included within System A on this table since it is described by those authors as lying within the Carl Creek Limestone.

Late Oligocene (Archer et al., 1995; Myers & Archer, this volume) System A may have been a time of 'icehouse conditions' with relatively low temperature, rainfall and biodiversity (Frakes et al., 1987).

Five macropodoid species have now been identified in System A sites. Of these, *Balbaroo gregoriensis* and *Wabularoo naughtoni* are known also from System B and *Bulungamaya delicata* occurs in sites in all 3 Systems. *Gumardee pascuali* and *Galanarla tessellata* are so far known only from System A. Unfortunately molar teeth preserved in the holotypes of the last two species are badly worn and/or damaged, reducing their usefulness for biostratigraphic analysis. However, lower molars of *Galanarla tessellata* exhibit a well-developed posterior cingulid linked to a postentocristid, a feature typical of balbarines (see Cooke this volume), but not present among bulungamayines.

G. tessellata is here assigned to the Balbarinae. As noted by Flannery et al. (1982), *Gumardee pascuali* is of comparable size to *Wabularoo naughtoni*, a common variable species within Riversleigh's Systems A and B. *G. pascuali* is considered to fall within the range of variation observed among specimens of *W. naughtoni*.

Nambaroo, *Wururoo* (Cooke, this volume) and *Ganawamaya*, *Balbaroo* sp.2, *Nowidgee matrix* (Cooke, this volume) and *Ganguroo bilamina*

(Cooke, this volume) all occur in System B, but not in System A or C. These taxa in newly discovered sites of unknown relative age may therefore be suggestive of an age comparable to other System B sites. Occurrence of *B. delicata* in all three systems and of *W. naughtoni* and *B. gregoriensis* in Systems A and B suggests that caution is indicated before declaring any of the above taxa, so far found only in System B, as definitive indicators of that System. *Balbaroo gregoriensis*, for instance, is more derived in molar morphology than any *Nambaroo* and it seems likely that representatives of the latter plesiomorphic balbarine and perhaps of others, such as *Wururoo* and *Ganawamaya*, may also ultimately be found in System A. If System B sites are correctly interpreted as early Miocene in age (Archer et al., 1994, 1995), remains found in those sites may have accumulated during 'greenhouse conditions' with high temperatures, rainfall and biodiversity (Frakes et al., 1987).

The macropodoid fauna of System C is more distinctive than those of Systems A and B, containing representatives of 5 subfamilies: 4 species of Bulungamayinae and 1 each of Hysiprymnodontinae, Potoroinae, Proploepinae and Balbarinae. Of the 8 macropodoid species known from System C, *Bulungamaya delicata* is the only one occurring in other Systems. Of the remainder, *Wan* (which includes the 'Gag Site macropodine' of Flannery, 1989) and *Ganguroo* sp.2 are among the most highly derived bulungamayines and *Balbaroo* sp.4 is more derived in molar morphology than any other known balbarine species. Presence of these species in particular in any given site may suggest but not define an age comparable to, or perhaps younger than that of System C sites. Archer et al. (1994, 1995) suggested that System C is middle Miocene. If this is so, this interval was also characterised by 'greenhouse conditions' (Frakes et al., 1987).

Overall macropodid faunal composition, rather than presence of particular species, may provide a more reliable guide in assessing relative ages of Riversleigh sites. If *Galanarla tessellata* is accepted as a balbarine and *Gumardee pascuali* as a bulungamayine, these subfamilies are represented in System A by 5 species, roughly equally divided among between the two: 3 bulungamayines versus 2 balbarines, with 7 identified specimens from each subfamily. System A deposits may thus be characterised by roughly equal diversity and abundance of balbarine and bulungamayine species.

The diversity of macropodoid species is greatest in absolute terms in System B. Balbarines and bulungamayines are both present, with balbarines dominating in terms of numbers of species (13 versus 4). If numbers of identified specimens are taken as a crude guide to abundance within species, bulungamayines appear to have been more abundant, the 3 species of lophodont bulungamayines being represented by a total of 102 specimens, compared to a total of 32 balbarine specimens from 12 species. System B deposits may thus be characterised by high species diversity of balbarines with accompanying low species abundance, and by a lower species diversity of bulungamayines but a relatively higher abundance of members of those species.

Subfamilial diversity is greatest in System C, but Potoroinae, Hypsiprymnodontinae and Propleopinae are each represented by single species. Among the lophodont species, bulungamayines have gained the ascendancy over balbarines in terms of numbers of species (4 versus 1) and in relative abundance (16 identified specimens versus 3).

System C may thus be characterised by dominance of lophodont bulungamayines, low incidence of balbarines and possible hypsiprymnodontines, propleopines and potorvines, although undescribed propleopine remains are known from sites such as Dirk's Towers which is probably equivalent in age to system B.

Lower absolute diversity in System A deposits may result from cooler, drier climatic conditions, exacerbated by the lower number of System A sites (2) yielding identified macropodoid species, compared to the number of System B sites (10) yielding such species. Macropodoid diversity within System A is thus likely to have been higher than that currently known.

System B deposits are suggested to have accumulated in pools or shallow lakes and System C deposits in deep pools, shallow pools or emergent accreting surfaces, or cave outwashes (Archer et al., 1994). Depositional environments are thus more comparable for Systems B and C. The probabilities of accumulating remains of terrestrial mammals are also likely to be comparable for these systems. Differences in overall macropodoid faunal composition between these two Systems are therefore more likely to be a true reflection of conditions prevailing during the times of deposition of these Systems.

There is a striking change in macropodoid faunal composition between Systems B and C. With the exception of a single, highly-derived lopho-

dont, *Balbaroo* sp.4, browsing balbarines are apparently absent from System C, as is *Wabularoo naughtoni* which persists through Systems A and B. *Bulungamaya delicata* persists only in sites low in the sequence of System C deposits. System B omnivores, such as *Nowidgee*, are replaced in System C by *Bettongia moyesii* and *Hypsiprymnodon bartholomaii*. Compared to System B, System C macropodoid assemblages are depauperate in numbers of species and dominated by larger, derived, lophodont bulungamayines whose long premolars and general molar morphology bear strong similarities to those of plesiomorphic macropodids. The System B macropodoid assemblages have a high species diversity, particularly among balbarines. High faunal diversity is a characteristic of rainforest habitats, suggested by Archer et al. (1989) to be the habitat for older Riversleigh local faunas (including those from System C). The decline in overall macropodoid diversity evident within System C and the dominance of larger, lophodont bulungamayine species suggests that rainforest habitat indicated by Archer et al. (1989) may have been in decline during accumulation of System C. That this was not a sudden event is indicated by the persistence of the presumably rainforest adapted *B. delicata* into the lower levels of System C at Gag Site, the occurrence at this same site of *Hypsiprymnodon*, modern representatives of which are confined to rainforest in northern Queensland, and the occurrence there of a high diversity of possum species (Archer et al., 1991).

Archer et al. (1994, 1995) estimated the age of System B as early Miocene and System C as middle Miocene. McGowran & Li (1994) correlate the planktonic foraminifera record of southern Australia, oceanic $\delta^{18}\text{O}$ levels and sea level fluctuations and indicate generally warmer, wetter climatic conditions during the Oligocene-early Miocene, with 3 warm and moist climatic optima occurring during the Miocene. Two of these occur during the early Miocene (during the Janjukian and Longfordian stages respectively, and a double-peaked optimum occurred during the early middle Miocene, corresponding with Batesfordian and Balcombian stages, 16-15ma. Following the latest of these climatic optima there is a general and world wide decline towards a cooler, drier climatic regime associated with a 'reverse greenhouse' effect. In northern Australia the effects of this decline would have been exacerbated by the middle Miocene uplift of the New Guinea Highlands. Archer et al. (1989) have sug-

gested these newly upthrust mountains could have created a 'rain shadow' effect across northern Australia which may have been one of the most important factors causing the decline of central and northern Australian rainforests. The climatic decline following the early middle Miocene climatic optimum coincides well with the early middle Miocene estimate of Archer et al. (1994, 1995) for the System B/C boundary. It is therefore likely that the decline in macropodoid diversity at the System B/C boundary is a reflection of the combined effects of the geological and climatic phenomena outlined above.

A number of Riversleigh sites are of uncertain stratigraphic relationship. The local biostratigraphic implications of the macropodoid taxa which have been found in some of these are discussed below.

The low stratigraphic position of White Hunter Site and its unusual faunal assemblage make it uncertain whether it belongs to System A or B. Of its 7 identified macropodid taxa found, 5 are unique to the site and, of themselves, do little to settle the question either way. Of the remainder, the plesiomorphic balbarine, *Nambaroo* sp.8, is found elsewhere only at Dunsinane Site whose relative age is also uncertain (but see Arena, this volume). *Nowidgee matrix*, is found only within System B at sites in both lower and higher levels of the sequence. The occurrence of this species and the overall composition of the macropodoid fauna of White Hunter Site — dominated by plesiomorphic balbarines with 2 plesiomorphic bulungamayines, suggests that the site is possibly a basal member of the System B sequence. The 2 species of *Nambaroo* found in this site are extremely plesiomorphic balbarines (Cooke, this volume) and the species of *Nowidgee* found there are similarly plesiomorphic bulungamayines (Cooke, this volume). Occurrence of such plesiomorphic species in the one site suggests that White Hunter may be even older, perhaps belonging to System A (Creaser, this volume). The latter interpretation is supported by Myers & Archer (this volume) who report the occurrence at White Hunter Site of *Kuterintja ngama*, an ilariid conspecific with one in the Mammalon Hill Local Fauna of central Australia that is dated as 24myo (late Oligocene) by magnetostratigraphy.

The occurrence of *N. sp.8* at Dunsinane Site complicates rather than clarifies understanding of this already enigmatic site in which are preserved plant material, insects and fossil bone. Dunsinane occurs in an area close to the boundary of the Tertiary limestone and Precambrian quartzite.

The occurrence of this plesiomorphic balbarine suggests the site may be equivalent in age to White Hunter Site, but there are several reasons for caution. No other vertebrate remains supporting this age determination have so far been identified from this site. All vertebrate remains here are fragmented and poorly preserved and may well have been re-deposited after previous re-working.

Bitesantennary Site and Dirk's Towers Site are both intrusive deposits on the D Site Plateau, regarded as probably equivalent to System B assemblages (Archer et al., 1994). Only a single macropodoid, *Ganguroo bilamina*, has been identified from Bitesantennary Site, but this species is otherwise known only from System B. Dirk's Towers Site has 3 macropodoids, including *Bulungamaya delicata*, known from Systems A, B and C. *Balbaroo gregoriensis* is known from both Systems A and B. However, *Nambaroo* sp.5, is known only from System B. On balance, macropodoid fauna of Dirk's Towers Site supports a System B age.

Archer et al. (1994) suggested that the faunal assemblage of Quantum Leap warrants its likely inclusion in System A. Only 3 macropodoid species are so far known from this site. *Bulungamaya delicata* is uninformative since it occurs in all 3 Systems. However, 2 species of *Nambaroo* are known from the site, both species otherwise known from System B sites or those likely to be of equivalent age, e.g., Dirk's Towers and Neville's Garden Sites. The macropodoid fauna of this site therefore suggests a closer affinity with System B rather than System A.

Neville's Garden Site is a possible cave outwash deposit considered to be equivalent in age to System B (Archer et al., 1994). Macropodoids of this site include the ubiquitous *B. delicata*, *W. naughtoni* and *Balbaroo gregoriensis*, the latter two occurring in systems A and B, and 2 species of *Nambaroo* known from both upper and lower levels of System B. The occurrence of the latter species and the typical System B composition of the Neville's Garden macropodoid fauna support a System B age for this site.

Dome Site, Jim's Carousel Site and Cleft of Ages Site have all been suggested to be younger than System C sites (Archer et al., 1994). *Gen.Wan. sp.1* (the 'Gag Site macropodine') is the only macropodoid so far identified from Dome Site. It is known elsewhere only from Gag Site in System C and Encore Site of possible late Miocene age (Archer et al., 1994). *Ganguroo* sp.2 is the only macropodoid so far known from Jim's

Carousel Site. This species is also known from Gag and last Minute Sites, low in the sequence of System C deposits, and from Henk's Hollow Site in the higher levels of that sequence.

Both species are highly derived bulungamayines which first appear in System C, but there is no reason to suggest that they may not have persisted beyond System C. Their presence in Dome and Jim's Carousel Sites therefore cannot confirm or deny the younger age postulated for these sites.

The single macropodoid, *Wururoo* sp.2, from Cleft of Ages is a plesiomorphic balbarine otherwise known only from System B. Its presence therefore suggests system B. This is in conflict with wombat teeth in this site, not known from any of the older Riversleigh sites, and the 'generally more modern' (presumably 'more derived') appearance of other remains (Archer et al., 1989).

Encore Site has been suggested to be younger still, possibly late Miocene (Archer et al., 1994). Encore has 2 highly derived bulungamayine species, gen. *Wan.*, spp. 1&2. Both species are known from System C, but there is no reason to suggest that these moderately robust, lophodont species might not persist beyond the age of that system. Their presence does not preclude the age estimated for this site.

MACROPODROID CORRELATES BETWEEN RIVERSLEIGH AND OTHER AUSTRALIAN TERTIARY FOSSIL AREAS OF COMPARABLE AGE

Archer et al. (1989) suggested that Riversleigh System A units may fall "somewhere between the Ditjimanka and Kutjumarpu and Tarkarooloo LF's of South Australia" a view supported by Woodburne et al. (1993). The latter authors maintained that the base of the mammal-bearing sequence in the Etadunna, Namba and Wipajiri Formations predates that of the Riversleigh succession. They noted in their (lowest) faunal zone A at Lake Palankarinna *Kyeema mahoneyi*, claimed to be the most plesiomorphic potoroid so far found. Formal description of this species has yet to be published and its level of evolutionary development therefore cannot be compared with any of the plesiomorphic Riversleigh potoroids.

Woodburne et al. (1993) also report 2 new species of *Nambaroo* — species A and B, both occurring in faunal zone C from the Ngapakaldi Local Fauna of the Etadunna formation, with species B also present in the Ngama Local Fauna in faunal zone D. Both species are described as

more primitive than *Nambaroo saltavus* and *N. tarrinyeri* from the Tarkarooloo Local Fauna, provisionally equated with zone D of the Etadunna Formation at Lake Palankarinna. Archer et al. (1989) correlated Riversleigh System B Local Faunas with the Tarkarooloo and Kutjumarpu Local Faunas. Woodburne et al. (1993) considered the Kutjumarpu Local Fauna of the Wipajiri Formation to represent the uppermost faunal unit in the eastern Lake Eyre Basin, and indicated a possible latest Oligocene age for this Local Fauna. M₁ morphology in *Nambaroo* sp.8 from White Hunter Site is more plesiomorphic than that of any of the *Nambaroo* species in the Tarkarooloo Local Fauna. It retains a hypoconulid, has a straight or only slightly curved paracristid, a short, low anterior cingulid, an under-developed precingulid and a diagonal posthypocristid on the posterior face of the hypolophid. Using the level of evolutionary development argument of Woodburne et al. (1993), the White Hunter assemblage would be older than either the Lake Tarkarooloo or Kutjumarpu Local Faunas, possibly of equivalent age to their zone B+C, estimated by them to be between 25.5–25.0myo. If White Hunter Site is a member of System B, System A sites at Riversleigh would therefore be older, possibly equivalent in age to zone A of the Etadunna formation, i.e., > 25.5myo.

Woodburne et al. (1993) reported a new genus and species of macropodid (their macropodine Gen. *P* sp. A.) from zone C of the Etadunna Formation

This species was described as more apomorphic in M₁ trigonid morphology than species of *Nambaroo*, having a 'reduced protostylid'. It was considered by them to be potentially ancestral to two new species of *Balbaroo* from the Kutjumarpu Local Fauna. Given this information the new genus must be a balbarine comparable to *Wururoo* (Cooke, this volume) from System B. The comparable levels of development of these genera provide further evidence for equating System B sites with zone B+C of the Etadunna formation. The overall high diversity of balbarine species reported from the various zones of the Etadunna Formation and from the Kutjumarpu Local Fauna (5 species of *Nambaroo*, 2 of *Balbaroo*, 3 of the balbarine genus *P*, and a species of a macropodine [possibly balbarine?] genus *W*) is, as has been noted above, typical of the high balbarine diversity of System B at Riversleigh and lends further support to a late Oligocene age for Riversleigh System B, its basal

units being probably equivalent in age to the Ditjimanka and Ngapakaldi Local Faunas of the Etadunna Formation.

At the opposite end of the time scale, derived, lophodont bulungamayines such as gen. *Wan.*, occurring in Riversleigh System C and possibly younger sites, have been suggested elsewhere (Cooke, this volume) to be likely antecedents of plesiomorphic macropodids such as *Hadronomas puckridgi* from the late Miocene Alcoota Local Fauna. Youngest Miocene sites at Riversleigh are therefore probably older than the Alcoota Local Fauna. *Balbaroo* sp.4 has lower molar morphology that is more derived than that of *B. camfieldensis* from the late middle Miocene Bullock Creek Local Fauna. *B.* sp.4 occurs in the highest levels of System C which may therefore approximate the age of the Bullock Creek Local Fauna.

Kangaroo fossils so far recovered from Riversleigh thus support an age span for pre-Pliocene deposits extending from late Oligocene to at least late middle Miocene. For some Riversleigh sites, e.g., Dunsinane and Clefi of Ages Sites, they suggest ages older than those previously indicated by Archer et al. (1994).

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OLIGOCENE-MIOCENE SEDIMENTS OF RIVERSLEIGH: THE POTENTIAL SIGNIFICANCE OF TOPOGRAPHY

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Although faunal assemblages provide the best indication of relative ages and environments of deposition in Tertiary and Quaternary sediments of the Riversleigh region, geological evidence provides additional significant information about the prehistory of the area. Data presented herein on topographic heights of sites in areas of horizontally-bedded sediments lead to an hypothesis of cyclical sedimentation. At least 3 cycles of Oligocene-Miocene sedimentation consist of 4 stages: 1) uplift and/or lowering of the water table; 2) erosion and development of a karst landscape; 3) subsidence and/or raising of the water table; and 4) sediment accumulation within the karst terrain and in surrounding shallow basins

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This paper uses data from Archer et al. (1989, 1994) and Megirian (1992), palaeontology and preliminary mapping using photogrammetric base maps at 1:2,000, 1:15,000 and 1:20,000 to interpret stratigraphy and palaeogeography of Oligocene-Miocene sediments at Riversleigh. I focus on Oligocene-Miocene sediments on D Site and Gag Plateaus dated primarily through biostratigraphy with magnetostratigraphically dated deposits in South Australia (Woodburne et al., 1994).

Archer et al. (1989) and Megirian (1992) focussed on D Site and Gag Plateaus, particularly Godthelp's Hill and Hal's Hill areas and the northern Gag Plateau. I concentrate herein on the northern D Site Plateau and the southern Gag Plateau. I also build on Archer et al.'s (1989) observation on the Gag Plateau that it is possible to correlate widely separated exposures of flat-lying sediments. In areas where the sediments are faulted or areas on the margins of microbasins where the beds are dipping, correlation is limited.

All sites have been plotted onto base maps lodged with the Vertebrate Palaeontology Laboratory, University of New South Wales, Queensland Museum and the Queensland National Parks and Wildlife Service. I provide new information on relative topographic heights which contributes to geological understanding of the region.

I consider geographic sections of each plateau and look at the geology of each section (Fig. 1) noting the range of sediment types, presumed age of the sediments based on palaeontological evidence and, where appropriate, topographic heights.

The other area considered is the 'Mesas', isolated erosional remnants of Tertiary sediment E

of the Riversleigh/Lawn Hill road. A number of these sites appear similar in lithology and stratigraphy to sites in the northern section of the D Site Plateau.

I recognise 3 sedimentary sequences (Verdon Creek, Godthelp's Hill and Gag Plateau). The Verdon Creek sequence is best represented in the northern section of D Site Plateau and consists of mainly System A sites (Archer et al., 1989). The Godthelp's Hill sequence occurs in the central section of D Site Plateau with System B sites. The Gag Plateau sequence is best represented in the northern section of Gag Plateau and contains mainly System C sites but may also include System A sites. Recent fieldwork has indicated a lack of uniformity and continuity of the basal sediments in the northern section of Gag Plateau.

D SITE PLATEAU

The northern section includes Neville's Garden/Burnt Offering area and the major gully system to the south of this area with sites such as Quantum Leap, Gillespie's Gully and MIM. It also includes sites on the eastern edge of the plateau (LSO and Dirk's Towers) as well as the sites on the western edge (BIB). The southern boundary is at or about Syp's Siberia Site to the north of Godthelp's Hill.

The central section includes Godthelp's Hill, Hal's Hill and other sites in the valley to the south east of these hills including White Hunter, ABRs, Sticky Beak and Wayne's Wok.

The southern section includes sites south of Hal's Hill commencing with the Biggles Flies Again Site, SM and TOTE Sites and Bone Reef, Jeanette's Amphitheatre and Chinatown Sites.

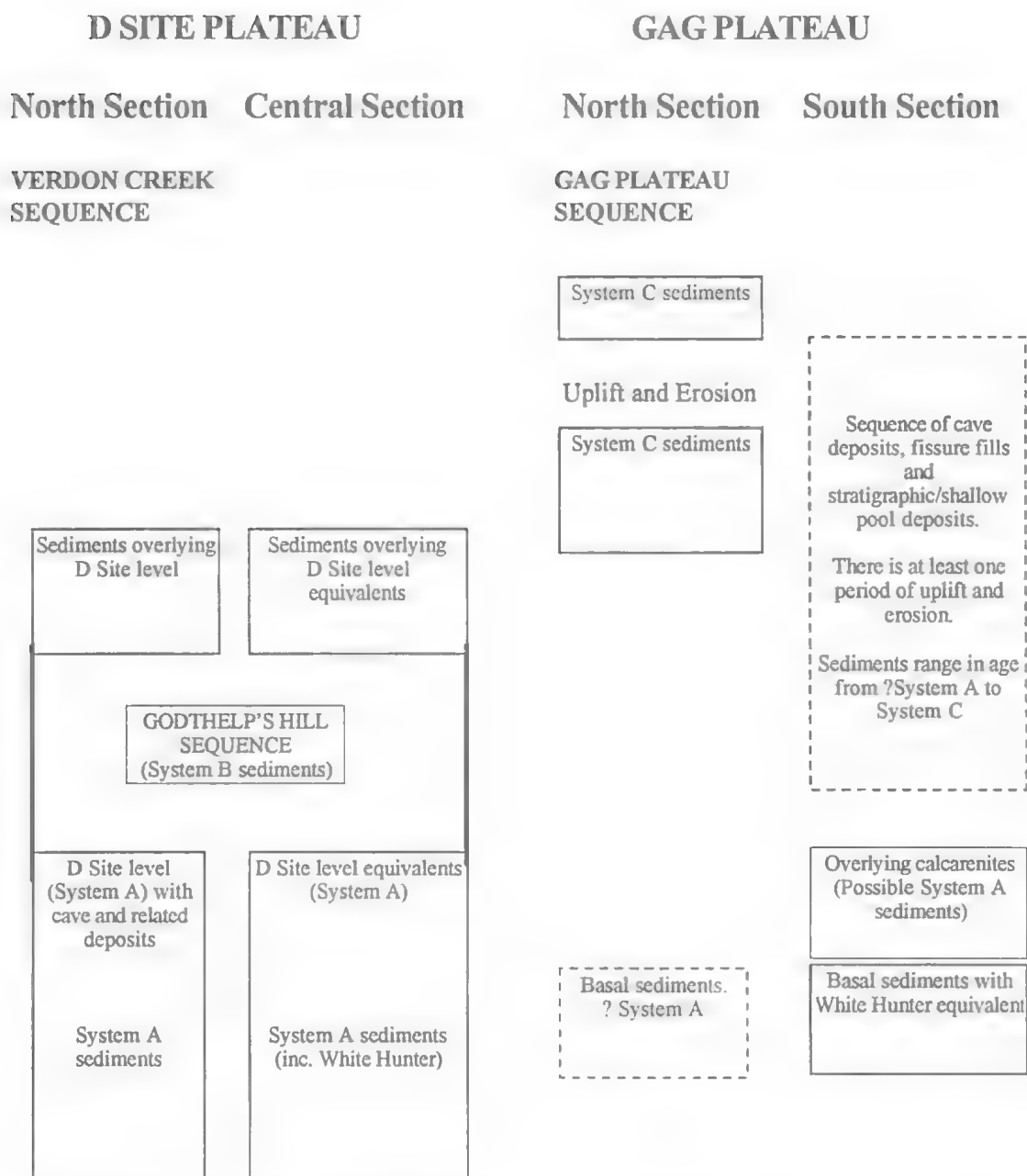


FIG. 1. Generalised Riversleigh stratigraphy based on geological observations, biocorrelations and topographic heights.

NORTHERN SECTION (VERDON CREEK SEQUENCE). This sequence is best seen in the area of Bitesantennary, Burnt Offering and Neville's Garden Sites where it consists of a basal conglomerate, overlain by arenites and calcarenites, up to 20m thick. A 3m homogeneous lime-

stone, the D Site Limestone, overlies these sediments. Cutting into and lying on the D Site Limestone are a series of cave deposits and possibly related tufa deposits. A further series of calcarenites are the highest units of this sequence.

The basal conglomerate consist of a series of

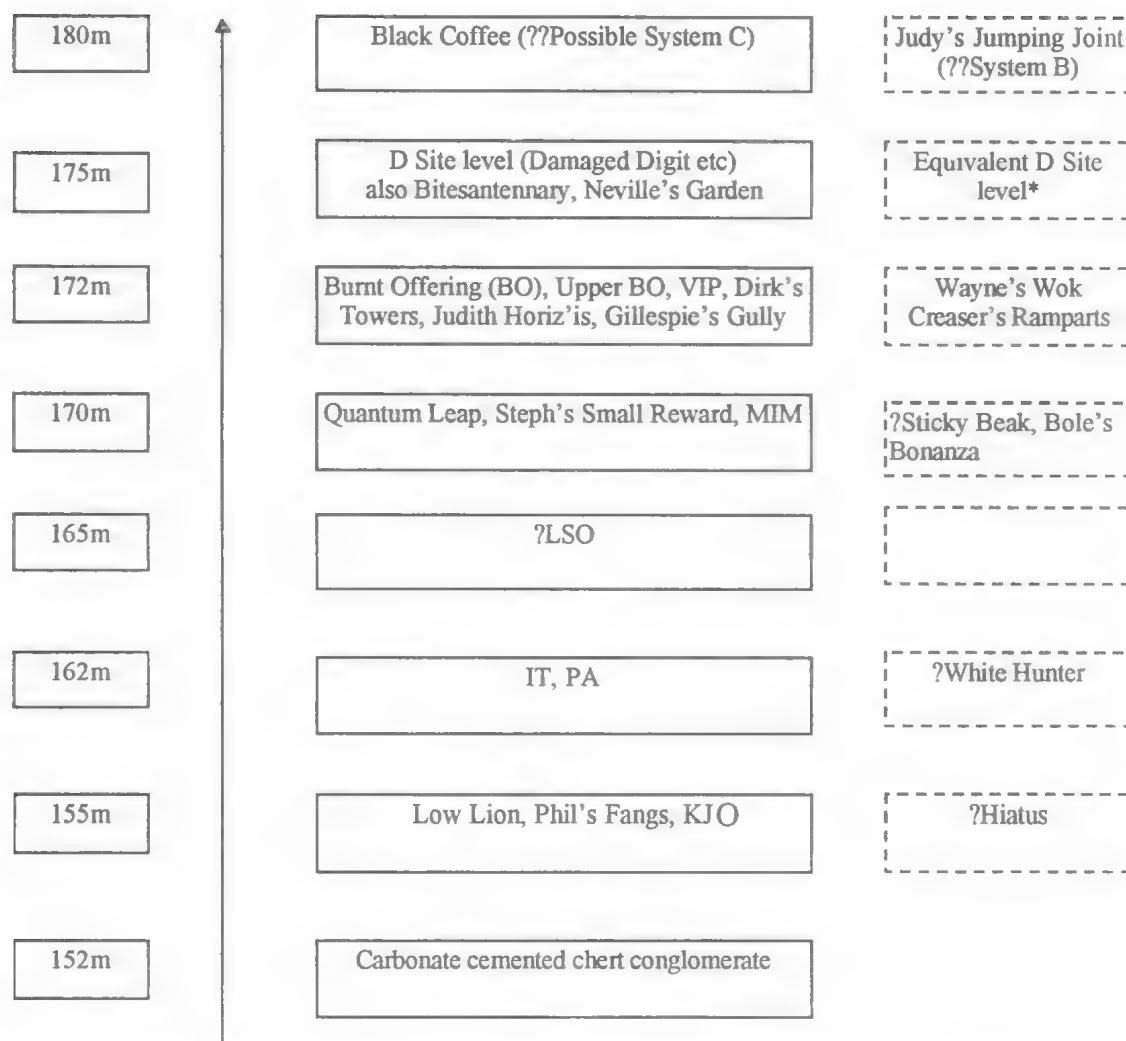


FIG. 2. Verdon Creek Sequence, System A with possible Systems B and C, 'type' section in northern section of D Site Plateau. Heights are in metres above sea level. Dashed boxes indicate relative positions of sites from the Hal's Hill area in the central section.

massive or normally graded, matrix-supported breccias and conglomerates and clast-supported cobble and pebble conglomerates (Megirian, 1992). Archer et al. (1989) questioned whether this conglomerate is contemporaneous throughout the region, suggesting that it could represent different, non-contemporaneous cycles of local weathering. The thickness of conglomerate varies considerably throughout the D Site Plateau.

There are several fossiliferous levels in the overlying arenites and calcarenites (Fig. 2) dominated by turtles, crocodiles, large birds and rare marsupials (usually diprotodontids).

The lowest level at the northern end of this section includes Low Lion and Phil's Fang Sites. A distinctive 25m wide fossiliferous horizon at the Low Lion level is at the same level as KJO Site. The level is dominated by large bone fragments similar in colour and preservation to fossils from Low Lion Site.

Above this level at the northern extremity of the Plateau are the IT and PA Sites which yielded jaw fragments of *Yalkaparidon*. These two adjacent sites, which contain small terrestrial assemblages, are the only ones known from the lower part of the sequence in this area. Although there

are other fossiliferous assemblages at about this level, they tend to consist of well-worn fragments of aquatic vertebrates.

The next fossiliferous level includes LSO Site. Above this are sites in the major gully in the northern part of this section including Quantum Leap, MIM and Steph's Small Reward Sites. Cooke (1997) considered the Quantum Leap Site kangaroos to be most similar to others from System A or B assemblages; its stratigraphic position and sedimentology suggest that it is a System A assemblage.

Above these sites but below the D Site Limestone level, is a higher more widespread fossiliferous level which includes Burnt Offering, Upper Burnt Offering, VIP, Judith Horizontalis, Punky Brewster, Gillespie's Gully and Dirk's Towers Sites. These appear to be stratigraphically controlled and do not represent a later incised deposit. While they are at the same topographic level and appear to be horizontally bedded, they may be of different ages.

Black (1997a) suggested that Burnt Offering is a System A site. Cooke (1997) suggested it might be a System B site; the macropodid fauna indicates that it could be either System A or B. Black (1997a) considered that Upper Burnt Offering is a System B site but *Neohelos* n. sp. 1 is only found in System A deposits. Black (1997a) considered VIP to be a System A site on the basis of a plesiomorphic zygomaturine. As yet, there is insufficient data from the Judith Horizontalis, Punky Brewster and Gillespie's Gully Sites to allocate these and no clear evidence from Dirk's Towers Site as to whether it is System A or B.

D Site Limestone is a distinctive marker bed that outcrops over much of the D Site Plateau and is characterised by a fossil assemblage of mainly large vertebrates dominated by mekosuchine crocodiles, dromornithids and diprotodontoids. However, the stratigraphy of D Site (Tedford, 1967) and of the ridge to the north of D Site, are less readily interpreted because of extensive scree slopes.

Archer et al. (1989) equated the D Site Limestone and its fossil assemblages with their System A. However, given further research since the mid 1980s and recognition of several fossiliferous levels well below this marker bed, it is recommended here that System A be expanded in concept to include all of the lower sediments of the Verdon Creek sequence.

A complex series of cave and possibly also tufa deposits have been etched into the D Site Limestone. This suggests a period of uplift or lowering

of the water table following deposition of the D Site Limestone, followed by karst weathering of the limestone to form caves and other sediment/fossil traps, and then infilling of these microbasins. The best known cave sites are Microsite and Bitesantennary Site with the best example of a tufa deposit being Neville's Garden Site with sediment and fossils accumulating at and beyond the entrance to a cave. However, Neville's Garden Site may represent a stratigraphically controlled site which can be correlated with Dirk's Towers or Judith Horizontalis Sites from this section or possibly Wayne's Wok and Creaser's Ramparts Sites from the central section of this Plateau. Black (1997) and Cooke (1997) assign this site to System B on its diprotodontoids and macropodoids respectively.

A thin series of calcarenites overlies the D Site Limestone and the cave and tufa deposits. However, fossils from these sediments are not common and only one site in this section, Black Coffee Site (above Gillespie's Gully), has been sampled. Its faunal assemblage has yet to be analysed in detail.

Topographically, the base of this sequence at the northern end of the Plateau is at 152m with the lowest fossiliferous level at about 155 m (Low Lion and KJO Sites). The base of the D Site Limestone is at 175m. The highest point on the D Site Plateau is at 202.7 m. Above Neville's Garden Site, the highest point is 192m which would give a thickness of at least 40m.

CENTRAL SECTION. The central section contains the discreet, richly-fossiliferous Godthelp's Hill sequence which is separated both stratigraphically and topographically from other sediments in this section which are similar in lithology and stratigraphy to the Verdon Creek sequence. The Godthelp's Hill sequence may be the equivalent of the cave and tufa deposits of the Verdon Creek sequence. The other sediments can probably be equated to the other Verdon Creek sequence sediments.

GODTHELP'S HILL SEQUENCE. Because they are separated, possibly due to faulting (Megirian, 1992), from the main sequence it is not clear whether the tufa deposits on Godthelp's Hill are the equivalent of the cave and related tufa deposits of the Verdon Creek sequence. Although faunal assemblages indicate a similar age, the Godthelp's Hill sediments, which have been regarded as System B (Archer et al., 1989), are regarded as a distinct sequence (Fig. 3). The

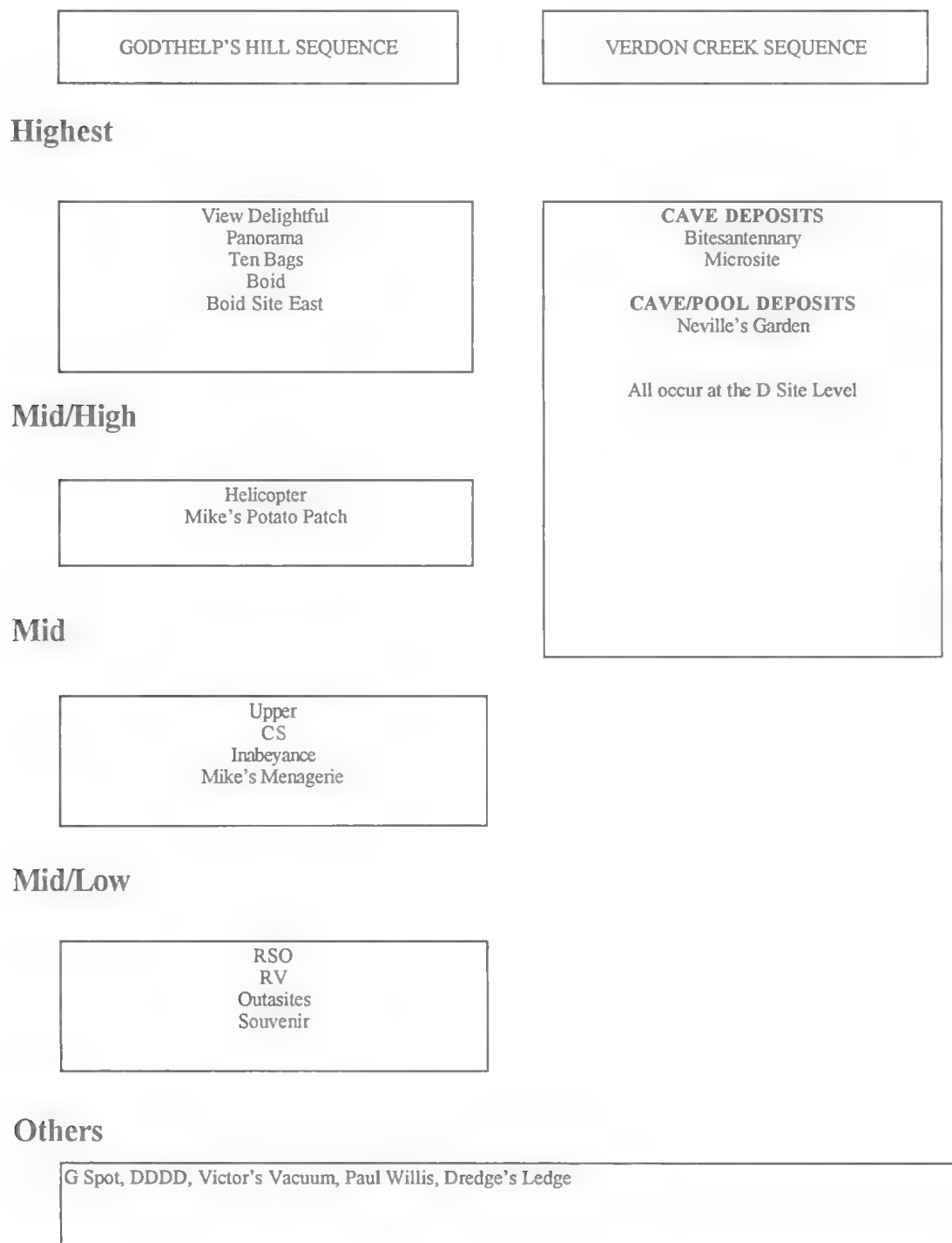


FIG. 3. Godthelp's Hill Sequence, System B with possible System B equivalents from the Verdon Creek Sequence.

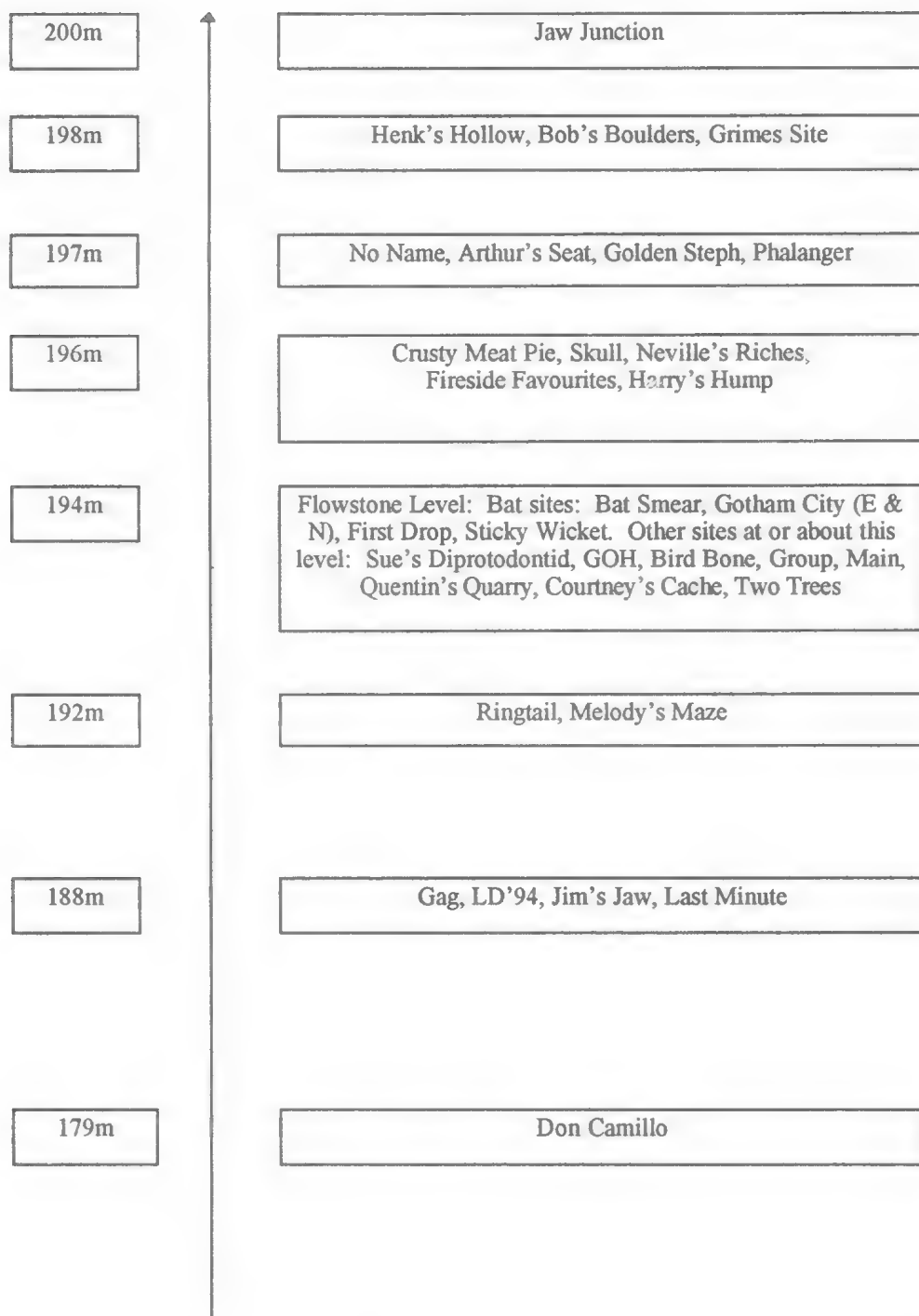


FIG. 4. Gag Plateau Sequence, System C, 'type' section in northern section of Gag Plateau based at Don Camillo Site. Heights are in metres above sea level. Sites to be plotted: Archie's Absence, Archie's Parlour, Bernie's Bedford, Kangaroo Jaw, Lockwood's Link, and Bruty and the Beast.

thickness of the sediments on Godthelp's Hill has been estimated to be 7m (Archer et al., 1989) to 12m (Megirian, 1992). Detailed photogrammetry of the area indicates that the estimate of 12m is more accurate.

OTHER SEDIMENTS IN THIS SECTION.

These sediments are around Hal's Hill to the south of Godthelp's Hill. Hiatus Site, the lowest in this area, is just above Precambrian sediments on the northern side of Hal's Hill. Although there is some doubt about its position because of faulting, it appears to be a base level. Black (1997a) notes that *Silvabestius michaelbirti* from Hiatus South Site is the most plesiomorphic zygomaturine known. Stratigraphic and topographic position and faunal assemblage suggest that White Hunter Site on the south side of Hal's Hill is very low in the sequence. However, its lithology differs from that of Hiatus Site and the basal sediments in the northern section of the Plateau. Black (1997a) indicates that Hiatus South Site belongs to System A. Cooke (1997) considers it a System ?A/B Site because several macropodoid species from White Hunter Site are also found in other undoubted System A and B sediments. However, there are also 5 unique macropodoid species from this site. Myers & Archer (1997) indicate White Hunter Site is the only one at Riversleigh that contains ilariids. Taken together, these suggest that White Hunter either represents a distinct interval of time or, if contemporaneous, a different ecosystem. I suggest that White Hunter Site is a basal System A deposit.

There are no distinctive fossiliferous levels immediately above either Hiatus or White Hunter Sites. The next site up section may be Sticky Beak Site which is a lower level than the D Site Limestone equivalent, approximately at the same level as Boles' Bonanza Site. Black (1997a) suggests that Sticky Beak Site belongs to System A.

The next level up is immediately below the D Site Limestone level equivalent. In this section, Wayne's Wok and Creaser's Ramparts Sites are at this level and may be correlated with Dirk's Towers and Judith Horizontalis Sites from the northern section. Both Black (1997a) and Cooke (1997) consider Wayne's Wok Site to be low in System B. However, this site contains a number of species that are found in Systems A and B. The age of Creaser's Ramparts Site is also unclear and more palaeontological information is needed. Black (pers. comm.) recognised a phascolarctid from this site, that is the most primitive from the Australian Tertiary.

In this section, the only D Site Limestone equivalent site is Neville's Pancake Site (with a plesiomorphic meiolaniid turtle; Gaffney et al., 1992). Fig Tree Site, with the most plesiomorphic zygomaturine *Nimbadon*; Hand et al., 1993 is stratigraphically below Neville's Pancake Site. Both sites are NE of Hal's Hill.

Above the D Site Limestone level, in the overlying calcarenites, only Judy's Jumping Joint site has been sampled. This site is a localised conglomerate found on the crest of Hal's Hill and belongs to System B. However, because the relationships are not clear, it is not possible to determine at present whether these calcarenites represent System A or B.

SOUTHERN SECTION. There has been relatively limited exploration in this section of the Plateau with preliminary fieldwork indicating a thin series of sediments. Sites such as Bone Reef and Jeanette's Amphitheatre are as yet largely unassessed. They are dominated by large animals more or less of the same kind (but far more abundant) that characterise the D Site Limestone at, for example, Site D. Black (1997a) considers these two sites System A deposits. Immediately below these are fossiliferous sediments. Two other sites collected from this region are Chinatown, which produced a System B assemblage, and a possible cave deposit with a rich bat fauna. SM and TOTE Sites, in the northern part of this section, are dominated by large vertebrates.

GAG PLATEAU

The northern section includes the vast range of sites at the northern end of the Plateau including Golden Steph, GOH, LD94 and First Drop. The central section is relatively barren apart from Wang Site and this relative lack of sites is its defining feature. The southern section includes AL90, COA, Dunsinane, Dome, JC, Encore and others. The northern boundary of this rich southern section is at Peter the Pilot Site.

NORTHERN SECTION (GAG PLATEAU SEQUENCE). Based on a composite section starting with Don Camillo Site at the base (near the northern point of this section), up through Gag Site to Jaw Junction Site at the top, together with equivalent sites at the appropriate levels at the northern end of this section, the Gag Plateau sequence was considered (Archer et al., 1989) to consist of fossiliferous basal sediments overlain by calcarenites and a series of tufa and 'deep water

'pool' deposits which, in some cases, contain diverse faunal assemblages. However, this sequence contains a complex variety of basal sediments. At Don Camillo site, which was considered the stratigraphic equivalent of the D Site Limestone, significantly different lithologies are present. At the eastern end of this section is a fossiliferous conglomerate and at the western end a vertical sequence of richly fossiliferous sediments. Overlying the Precambrian is a thin sequence of arenaceous sediments overlain by fossiliferous calcarenites which in turn are overlain by (?) weathered lateritic sediments. These are overlain by the 'typical' calcarenites which in some places have rich vertebrate assemblages. However, none of these sediments are apparently continuous across the northern section of the Gag Plateau. Some of these basal sediments may be lateral equivalents of System A sediments in the Verdon Creek sequence.

While the basal sediments vary considerably, there is apparently more uniformity higher in the sequence including the tufa and 'deep water pool' deposits of Archer et al. (1989). The tufa deposits such as Gag, Henk's Hollow and Golden Step Sites, are dominated by terrestrial faunas. In contrast, the 'deep water pool' deposits, such as Crusty Meat Pie, Quentin's Quarry, Bob's Boulders and Ringtail Sites are dominated by aquatic faunas.

Don Camillo Site is at approximately 179m with the highest point at 201m (Jaw Junction Site), giving a maximum thickness of 22m assuming the beds are horizontal. Gag, Last Minute and LD'94 Sites are all at 188m with the erosional break recognised by Archer et al. (1989) and Megirian (1992) at 194m. The only sites with significant bat accumulations (Gotham City, Sticky Wicket, Bat Smear and First Drop Sites) are found at this level (Fig. 4).

CENTRAL SECTION. Only Wang Site is known from this section, with no clear 'dividing line' between the northern and southern sections. However, sediments in the southern section differ in the type and extent of their lithologies and faunas.

SOUTHERN SECTION. The stratigraphy of this section is complex. Unlike the northern section of the D Site Plateau or the upper northern section of the Gag Plateau, the series and types of sediments in the southern section are apparently not limited in lateral extent, often significantly different in age and do not appear to be horizontally

bedded. This makes it particularly difficult to correlate this section with others (Fig. 5). Palaeontological evidence from this section allows some correlations.

The oldest recognised sediments are at Dunsinane Site (and equivalents) with plant and animal fossils. These sediments are overlain by less fossiliferous calcarenites into which are incised richly fossiliferous cave and fissure fill deposits.

Dunsinane, Sue's Rocky Road, Custard Tart and Bernie's Cooking Pot Sites may represent the oldest from the Gag Plateau, possibly System A, on the basis of correlation of mammals with White Hunter Site (Arena, 1997; Cooke, 1997).

Fossils are not common in the overlying calcarenites at Anna's Horribilis, Two Gloves, Anton's Pixie, Arachnid Ridge and Don't Ask Me Sites, all of which have yet to be studied in detail but are probably System A sites. Faunas and lithologies indicate cave deposits at Dome, AL'90, Peter the Pilot, Creaser's Crouch and Angela's Bat Pate Sites. Fissure fill deposits such as COA and Keith's Chocky Block Sites are easily recognisable because of their lithologies. Jim's Carousel and Encore Sites could represent tufa deposits incised into a pre-existing Tertiary limestone.

While the lithologies and environment of deposition of many of these sites are similar, it is clear that they represent a wide range of ages. Black (1997a) suggests that AL'90, Jim's Carousel and Dome Sites may all be System C deposits. Black (1997a) suggests that COA Site may be a System A site, but Cooke (1997) suggests it is either System A or B. A. Gillespie (pers. comm.) considers it to be System B. Encore Site despite being lithologically very similar to other sites in the area, is early late Miocene, System C (Archer et al., 1994; Black, 1997b).

ENVIRONMENTS OF DEPOSITION AND PALAEOGEOGRAPHY

The Tertiary limestone deposits of the Gregory River area are freshwater fluvio-lacustrine deposits. Archer et al. (1989) recognised a complex series of lacustrine, alluvial, travertine and cave deposits while Megirian (1992) has documented alluvial, tufa and karst facies.

I agree with these views and propose that a cycle of sedimentation/erosion that involves: 1, uplift and or lowering of the water table; 2, erosion and development of a karst landscape; 3,

Central Section

Wang Site

Southern Section**Cave Deposits**

Peter the Pilot,
Creaser's Crouch (CC)
Upper CC
Nicole's Boulders W
AL'90
Captain Androgen
Jolly Roger
Bernards Belted Belfry
Angela's Bat Pate
Bat Eerk
Anne's Bat Room
Dome (N & S)
Jeanette's Bat Stuff

Fissure fills

COA
Keith's Chocky Block

Stratigraphic/Shallow Pool Deposits

Arachnid Ridge*
Nicole's Boulders
JC Sites
Not JC8
Anna's Horribilis*
Two Gloves*
Encore
Angela's Sinkhole
Don't Ask Me*
Anton's Pixie*

Dunsinane, Custard Tart, Sue's Rocky Road,
Bernie's Cooking Pot
Equivalent to White Hunter Site on D Site
Plateau

FIG. 5. Gag Plateau Sequence, central and southern sections. The age of these sites is unclear (apart perhaps from Dunsinane Site and its equivalents) although there is evidence that there is a range of different ages represented. Deposits marked * appear to represent faunas from the calcarenites which overlie the Dunsinane Site and its equivalents.

subsidence and or raising of the water table; 4. sediment accumulation within the karst terrane and surrounding basins. This 4-stage cycle occurred at least 3 times during Oligo-Miocene time at Riversleigh. Each new cycle may have been initiated by minor tectonic activity that may have been responsible for changes in the hydrogeologic system. Megirian (1992) noted faulting on Godthelp's Hill which may have been responsible for deposition of the basal conglomerates as a debris flow.

Following initial observation by B. Cooke that Tertiary limestone on the mesas not uncommonly rest directly on Precambrian quartzite, M. Archer

demonstrated that there did not appear to be anywhere on either the D Site Plateau or the Gag Plateau where Tertiary sediments directly overlay the Cambrian limestones. In a number of places, however, Tertiary sediments can be found adjacent to Cambrian limestones (e.g. Microsite which is topographically situated between a high of Thornton Limestone to the west and D Site Limestone to the east) which suggests that karst topography of Cambrian limestones may have controlled sedimentation patterns in the Tertiary.

I suggest that the basal arenaceous sediments and the overlying calcarenites were deposited in an alluvial fan/braided stream environment.

Given the outcrop pattern, it is likely that the streams flowed in a northeasterly direction. As Megirian (1992) has noted, fossils are not common in this type of environment. However, in some parts of this environment, possibly in swamp areas or stagnant water away from the forest, assemblages of large aquatic and terrestrial animal fossils accumulated. In other areas freshwater limestone tufa pools developed in or at the edge of the rainforest but these are relatively rare. The level containing rich faunas from sites such as Dirk's Towers, Creaser's Ramparts, Judith Horizontalis and Burnt Offering Sites, is a notable example. These sites are often found in gullies today because they are more easily weathered than the surrounding more resistant sediments. There does not appear to be any breaks in this part of the sequence and it is suggested that this sedimentation continued until (?) tectonic activity or a raised water table led to the empondment of larger lacustrine bodies of water in which accumulated the sediments (e.g., the D Site Limestone) exposed at localities such as D Site. These sediments are fairly uniform in lithology apart from the northeastern corner of the D Site Plateau (near the Lawn Hill road and Verdon Creek) where there is a high percentage of quartz grains suggesting a Precambrian source to the northeast. Large vertebrates, including crocodiles and turtles, are common in this limestone which is considered to represent an open lake or swamp, at some distance from the rainforest. This would explain the scarcity of terrestrial faunas especially when compared to the shallow pool tufa deposits (Archer et al., 1989).

Renewed tectonic uplift and/or a lowering of the water table resulted in renewed development of a karst landscape in the Tertiary as well as Cambrian limestones. This enabled formation of caves and their subsequent filling with fossiliferous deposits (e.g. Microsite and Bitesantennary Site), as well as deposits formed at cave entrances (e.g. Neville's Garden Site where fragments of speleothems (straws) and in situ travertine rills and small stalagmites have been found).

Godthelp's Hill sequence is regarded as a separate unit, which may be equivalent in part to these cave deposits. Lithology of the sediments and the fossils from sites on Godthelp's Hill suggest tufa deposits that accumulated over a period of time.

The uppermost series of calcarenites in the Verdon Creek sequence suggest a return to the alluvial braided stream facies, possibly following erosion of the karst landscape. These sediments

may be the lateral equivalents of the System C sediments at the northern end of the Gag Plateau, or alternatively they may be part of System A. System B faunal assemblage from the conglomerate at Judy's Jumping Joint Site does not enable any definite conclusions to be drawn because the relationship of this Site to the surrounding sediments is unclear.

The basal sediments at the northern end of the Gag Plateau vary from fossiliferous conglomerates to arenaceous sediments and weathered lateritic sediments. These sediments are overlain by calcarenites that suggest an alluvial braided stream facies, and a fossil-rich tufa and deep pool (aquatic) deposits. Like similar deposits in the Verdon Creek sequence, the tufa deposits appear to have accumulated in and around shallow terrestrial pools. There is no clear pattern evident in the distribution of these two types of shallow water tufa and deep water deposits. There is also a significant erosional break in the sequence that can be recognised in the field by flowstone and travertine deposits. Palaeontological evidence also indicates a significant break between the upper and lower parts of the sequence in this area and it may be no coincidence that the only sites in this area which contain significant bat accumulations are at this level. This suggests another cycle of uplift and/or lowering of the water table, cave development, cave fill, and erosion before sedimentation recommenced.

In contrast, there are apparently no similar sequences of shallow water tufa or deep pool deposits at the southern end of the Gag Plateau. Isolated sites such as Jim's Carousel Site, however, may be of this type. It is not clear if the sediments at the northern end are equivalent to the main sequence of sediments at the southern end of the Plateau.

Mammals from Dunsinane and related sites at the southern end of the Plateau, which appear to represent basal sediments, suggest correlation with White Hunter Site, a probable System A assemblage (Arena, 1996, 1997). These sediments are overlain by a series of calcarenites which were probably deposited in an alluvial fan/braided stream environment. Associated with the calcarenites are cave and fissure fill deposits which have been incised into the earlier Tertiary limestones indicating that a karst landscape had already been formed. The age of these cave and fissure fill deposits appears to range considerably with some (e.g., Encore Site) being the youngest Oligo-Miocene sediments in the region.

PALAEOENVIRONMENT

On the basis of the fossil faunas, Archer et al. (1989, 1994) suggested that rainforest covered the region at least during the early to middle Miocene. Archer (pers. comm., 1996) suggests that there is much less faunal evidence for rainforest being ubiquitous during the late Oligocene. Other researchers support this view although there seems to be evidence that this rainforest was unlike any found in Australia today and that the rainforests of New Caledonia or mid-montane Papua New Guinea may be more similar. Boles (1997) and White (1997) suggest that there were some patches of open forest. Megirian (1992) suggested the rainforest was a refugium confined to the proximity of perennial, spring-fed streams. He concluded that the palaeoclimate was relatively dry, perhaps semi-arid, despite the fact that the sediments were considered to be characteristic of humid alluvial fans. Archer et al. (1995) refuted this suggestion on faunal evidence. Creaser (1977) has also showed that although calcilithites, terrigenous clastic rocks in which carbonate fragments dominate, form mainly in alluvial fans in arid/semi-arid and glacial/periglacial environments, they are also forming today on the Huon Terraces in Papua New Guinea where tectonism and climate both appear to influence the accumulation of the calcilithites. The Huon Terraces are in a rainforest environment with 2000-2500mm of rain per annum. The rainfall has a marked peak in December to February, with the nearby mountain ranges forming a rainshadow, and a pronounced dry season at other times of the year. While there are differences between the Huon Terraces and the Gregory River region, it is possible for a species-rich rainforest to exist in an area of tectonic activity and produce the full range of sediments evident in the Gregory River basin. Although there is no evidence for seasonality in the early to middle Miocene sediments of Riversleigh, growth rings in wood fragments (*Nothofagus* sp.) from Dunsinane Site suggest seasonality (Jane O'Brien, pers. comm.) or at least episodic changes in growth rates. Unfortunately, the age and relative stratigraphic position of these fragments is in doubt (Arena, 1997). They could be either late Oligocene or late Miocene, both icehouse intervals (Frakes & Macgowran, 1987) when rainforest is less likely to have characterised the region. The plants of Dunsinane Site may have grown on the edge of a forest clearing, surrounding the Dunsinane body of water.

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PALORCHESTES AZAEL (MAMMALIA, PALORCHESTIDAE) FROM THE LATE
PLEISTOCENE TERRACE SITE LOCAL FAUNA, RIVERSLEIGH, NORTHWESTERN
QUEENSLAND

A.C. DAVIS AND M. ARCHER

Davis, A.C. & Archer, M., 1997 06 30. *Palorchestes azael* (Mammalia, Palorchestidae) from the late Pleistocene Terrace Site Local Fauna, Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 315-320. Brisbane. ISSN 0079-8835.

A maxilla of *Palorchestes azael* is described from gravel deposits at Terrace Site, Riversleigh Station. A radiocarbon date of 23,900 \pm 4100 -2700 years BP is reported from the fossiliferous unit at Terrace Site supporting previous interpretations of a late Pleistocene age for the Terrace Site Local Fauna.

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Terrace Site occurs in unconsolidated fluvialite sediments on the eastern bank of the Gregory River 5 km downstream from the Lawn Hill road crossing on Riversleigh Station, NW Queensland. These deposits were interpreted as Pleistocene gravels resting on Tertiary and Cambrian limestones (Archer et al., 1989, 1994). The Terrace Site Local Fauna is listed in Archer et al. (1994).

Material is deposited in the Australian Museum (AMF), the Natural History Museum, London (BM), Museum of Victoria (NMVP), Queensland Museum (QMF), South Australian Museum (SAM), Department of Geology, James Cook University (P). Molar number follows Luckett (1993); premolar number follows Flower (1867); molar crown morphology follows Archer (1984).

STRATIGRAPHY AND AGE

Terrace Site has a 3m high cross-section through horizontal and lenticular beds in an upwardly fining sequence. The basal sediments are poorly sorted, light grey sands and gravels with abundant mussel shell fragments and most of the vertebrates including QMF30882. The section grades upwards into finer sands, silts and clays with finer shell fragments. Charcoal particles up to 5mm occur throughout in small lenses or isolated fragments. The charcoal occurring in lenses, maxilla and most other specimens being un-abraded and the recovery of articulated material, suggests that at least part of the fauna and associated charcoal is a primary accumulation.

Based on the mammal fauna the age was inter-

preted as possibly late Pleistocene (Archer et al., 1994). Charcoal from the basal bone-rich layer that contained QMF30882 gave a conventional radiocarbon date of 23,900 \pm 4100 -2700 BP (ANU-7620). Although the standard errors are high, the range within two standard errors confirms the Late Pleistocene age.

SYSTEMATICS

Order DIPROTODONTIA Owen, 1866
Suborder VOMBATIFORMES Woodburne,
1984

Family PALORCHESTIDAE Tate, 1948 sens.
Archer & Bartholomai, 1978

Palorchestes Owen, 1873

TYPE SPECIES *Palorchestes azael* Owen, 1873.

Palorchestes azael Owen, 1873
(Fig. 1; Table 1)

MATERIAL. QMF30882, a left maxillary fragment with near complete M¹⁻³, the fragmented alveolus of P3, and a portion of the palate and jugal.

DESCRIPTION. Upper molars high-crowned, bilophodont, trapezoidal in occlusal view, with the protoloph wider than the metaloph. Lophs broad at their bases, narrow toward the apices, slightly crescentic. Broad anterior and posterior cingula on each tooth, extending around the tooth forming narrow lingual and buccal cingula. Molar enamel crenulated and rough on anterior, posterior and inter-loph surfaces, but smooth on lateral surfaces.

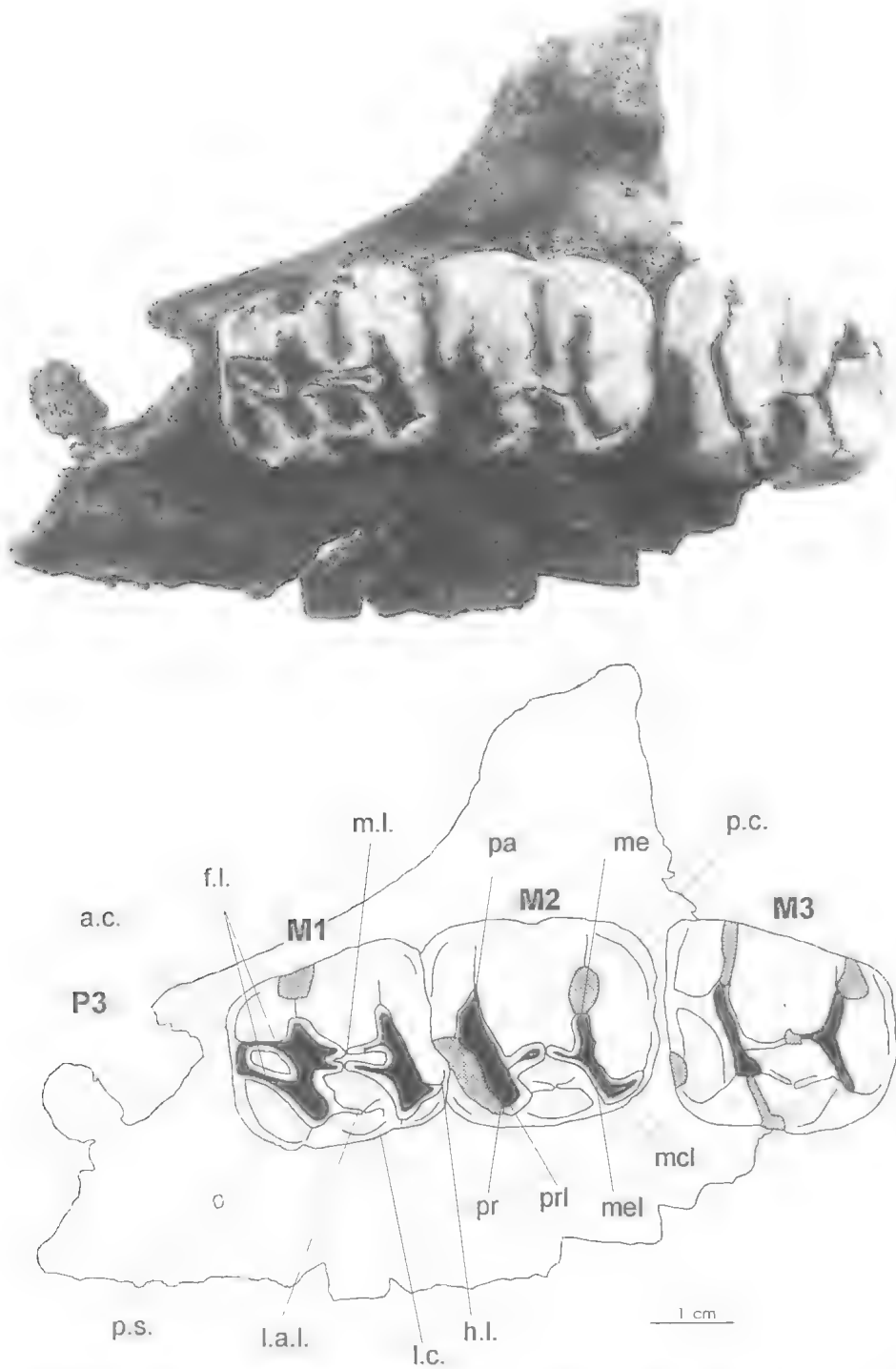


FIG. 1. *Palorchestes azael* Owen, 1873, QMF30882 from Terrace Site, maxillary fragment with M¹-M³, in occlusal view. a.c.=anterior cingulum; p.c.=posterior cingulum; l.c.=lingual cingulum; f.l.=forelink; m.l.=mid-link; h.l.=hindlink; l.a.l.=lingual accessory link; pr=protocone; pa=paracone; me=metacone; mcl=metaconule; prl=protoloph; mel=metaloph; p.s.=palatal sinus.

Table 1. Dimensions (mm) of upper cheek teeth of QMF30882 and comparative samples of *P. azael* (BM46316, AMF452, P186593, AMF7272, QMF7074, QMF772), *P. parvus* (from Woods 1958), *P. painei* (from Woodburne, 1967) and *P. selestiae* (from Mackness, 1995). The dimensions of the holotype of *P. azael* equal the minimum values of the observed ranges. e = estimate; H=holotype.

		QMF 30882	<i>P. azael</i>			<i>P. parvus</i>			<i>P. painei</i>			<i>P. selestiae</i> (H)
			N	MEAN	RANGE	N	MEAN	RANGE	N	MEAN	RANGE	
P ³	L	17.0e	2	20.8	18.7-23.7	1	16.8	-	4	13.9	13.8-14.4	-
M ¹	L	28.8	6	26.3	23.5-28.7	4	19.6	17.5-22.1	4	17.4	16.5-18.2	22.6
	AW	24.1e	6	23.0	19.3-27.7	4	15.5	14.2-17.3	4	14.2	13.6-14.4	16.6
	PW	23.5	6	21.9	17.1-23.0	3	-	-	3	13.5	13.2-13.8	16.9
M ²	L	29.2e	5	27.2	24.9-29.2	3	20.1	18.7-20.6	3	18.1	17.8-18.1	-
	AW	27.2	5	24.5	21.5-26.8	2	16.3	15.0-17.5	2	15.4	14.8-15.5	-
	PW	24.7	5	22.3	19.9-24.7	3	-	-	3	13.6	13.1-14.3	-
M ³	L	31.5	4	27.4	25.3-31.8	4	21.0	19.6-22.3	4	18.5	18.0-19.4	-
	AW	26.2	3	22.6	19.7-26.0	3	16.6	15.9-17.3	3	15.3	15.0-16.3	-
	PW	24.7	3	20.5	18.1-23.1	4	-	-	4	13.3	12.6-14.1	-
M ¹ -M ³	L	35.2	3	29.5	24.0-36.4	-	-	-	-	-	-	-

P³ missing. Partly preserved alveolus suggesting P³ as subtriangular, about 17 mm long.

M¹ nearly complete, missing only a small part of the enamel of the buccal side of the proto-loph, with 2 high forelinks joining the proto-loph to a broad anterior cingulum. Lingual forelink offset diagonally, joining the anterior cingulum from the protocone at the midline of the tooth. Deep pits between, and on both sides of, the forelinks. A high double-midlink between the lophs. On the lingual side of the double-midlink is an accessory link forming a deep lingual pit. Lingual accessory link high and well-developed on M¹. Posterior cingulum compressed by molar crowding from M²; an irregular folded posterior face of the metaloph formed from a thickened crest (hindlink) descending posteriorly from the metaconule.

M² larger than M¹, missing the anterolingual face of the proto-loph, with a single weak forelink, and midlink a single (cf. double in M¹) high link following the midline of the tooth. Lingual accessory link V-shaped in lateral view, differing from the straighter link of M¹ and slightly lower. Anterior and posterior cingula well-developed; anterior cingulum pressed into M¹ because of molar crowding. Hindlink present.

M³ similar in size and morphology to M², differences in length being attributed to molar crowding. Forelink, midlink and hindlink all single. Lingual accessory midlink more reduced than in M².

Base of the jugal projecting perpendicular to the maxilla, its anterior edge originating at the M¹-M² contact before sloping gradually posteri-

orly, with its posterior edge perpendicular to the maxilla at the M²-M³ junction. A few fragments of the orbital surface preserved on the upper part of the specimen. A minute palatal sinus level with the posterior edge of P³ alveolus 12 mm from the lingual edge of the tooth row. Only the left side of the palate preserved, extending from the tooth row to near the midpalatal suture.

COMPARISON. QMF30882 compares well with Woods (1958) diagnosis for *P. azael* and its molar dimensions (Table 1) lie within the ranges for *P. azael* and outside those of other species of *Palorchestes*. When compared with a cast of the holotype (BM46316) and description by Owen (1873, pl. 82 fig. 1), the Riversleigh specimen is larger in all dimensions but is otherwise similar. The holotype is the smallest of the comparative sample of *P. azael* examined.

QMF30882 is most similar to AMF452, from Wellington Caves (Dun, 1893, pl. 16), in which the only notable difference is the lingual accessory midlink being only slightly developed in M¹, less so in M² and absent in M³. QMF30882 shows a similar gradient of development from well-developed anteriorly to simplest posteriorly. QMF772 (Woods, 1958, fig. 1) also shows a lingual accessory midlink gradient, and is intermediate in development between the other two specimens. SAMP31370 and 31371 (Pledge, 1991, fig. 4) also show the lingual midlink. P186593 from the Wyandotte LF (McNamara, 1990) does not show the midlink at all, and it is unclear in the worn holotype BM46316 and AMF7272. The extreme expression of this char-

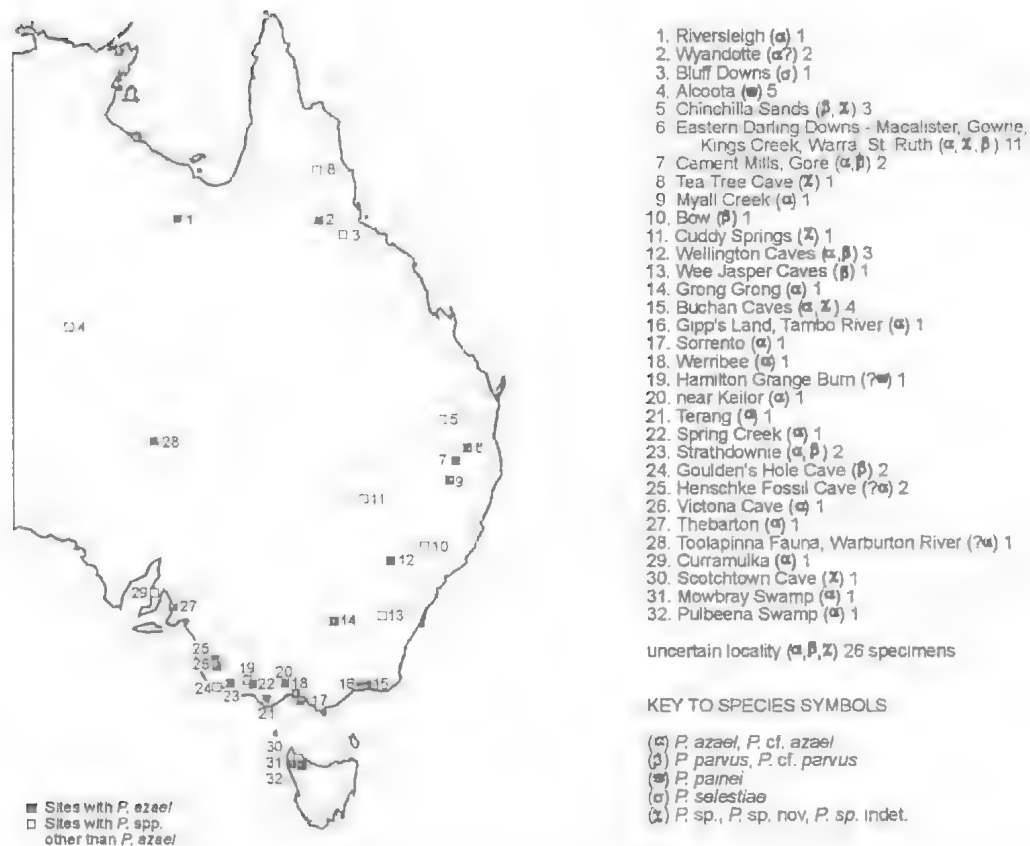


FIG. 2. Distribution of *Palorchestes* in Australia. The minimum number of individuals at each site (number after the species symbol in the site listing) includes published and unpublished specimens.

acter in QMF30882 is within the intraspecific range of variation.

The large variation in molar size for *P. azael* (Table 1), coupled with intraspecific variation support Woods' (1958) view that it is a highly variable species. Molar morphology grades along the tooth row from complex anterior molars with additional links to simple diprotodontid-like teeth posteriorly. Sample sizes are too small to estimate coefficients of variation for molar dimensions, or identify sexual dimorphism.

The Riversleigh specimen is larger than *P. parvus* from the early Pliocene Chinchilla Sand (Woods, 1958) (Table 1). Its molars are relatively broader resulting in squarer molars in occlusal view. The lack of a double hindlink on the M¹ as in QMF789 (Darling Downs; Woods, 1958, fig.4) and NMVP48987 (Buchan Caves) also distinguishes the two species.

The Riversleigh specimen differs from *P.*

selestiae, from the early Pliocene Bluff Downs Local Fauna (Mackness, 1995), in being about 25% smaller and in the lingual forelink being in contact with the anterior cingulum rather than terminating in the cingular basin.

It differs from *P. painei*, from the late Miocene at Alcoota (Woodburne, 1967) in being significantly larger (Table 1), with more complex molar morphology including higher crowns, having a double forelink on M1, and in having a single midlink on M2.

DISCUSSION. Over 80 Plio-Pleistocene *Palorchestes* specimens have been registered with museums from at least 32 open sites and cave deposits throughout Australia (Fig.2). *P. azael*, the most widely distributed species, is present in 21 of the 32 sites.

Few sites with *P. azael* have radiocarbon dates available. Published dates range from

19,800±390 BP at Spring Creek (Flannery & Gott, 1984) to 54,200 +11,000 -4,500 BP at Pulbeena Swamp (Banks et al., 1976) and 30,400 +750 -700 BP at Wyandotte (McNamara, 1990). Specimens at Wellington Caves, Naracoorte Caves (Wells et al., 1984) and the Warburton River (Toolapinna Fauna; Tedford et al., 1992) could be considerably older.

The presence of 2 species of *Palorchestes* at Cement Mills (Bartholomai, 1977), Wellington Caves, Buchan Caves, and Strathdownie (Flannery & Archer, 1985) has been interpreted by some to mean that they are mixed Pliocene and Pleistocene assemblages. Alternatively *P. parvus* may have extended into the Pleistocene as suggested by Bartholomai (1977) or Pleistocene *P. parvus* may be incorrectly assigned.

Although widespread, *P. azael* specimens are rare at any one site, generally being represented by only one or two individuals and no other fossils (at least 8 known sites) or a single specimen of *P. azael* with associated faunas (at least 8 sites). The low density may be an artefact of preservation, but could indicate that *P. azael* was a solitary animal (Flannery & Archer, 1985).

At Terrace Site *P. azael* is associated with the large to medium-sized herbivores in a fauna dominated by riverine turtles, crocodiles, water rats and fish (Archer et al., 1994). The palaeoenvironment is interpreted to have been similar to that which characterises the area today (Archer et al., 1994). The other northern Queensland assemblage, the Wyandotte Local Fauna (McNamara, 1990), contains a similar faunal assemblage. More southern faunas are dominated by large browsing and grazing mammals (e.g. *Diprotodon optatum* and diverse *Macropus*, *Protemnodon* and *Sthenurus* spp.) in open sclerophyll forest (Bartholomai, 1977), *Eucalyptus* woodland (Banks et al., 1976), low heath (Flannery & Gott, 1984) and trees & shrubland (Dodson et al., 1993). *P. azael* evidently tolerated a wide range of climatic conditions and habitat types.

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land Museum, the Australian Museum, Century Zinc (particularly Doug Fishburn), MIM, the Mount Isa City Council, Surrey Beauty & Sons, the Riversleigh Society, private supporters including Elaine Clark, Sue & Jim Lavarack, Sue & Don Scott-Orr, Margaret Beavis and Martin Dickson; research colleagues notably Henk Godthelp, Suzanne Hand, Alan Bartholomai, Phil Creaser, Peter Murray, David Ride, Sue Solomon, Arthur White, Anna Gillespie, Virginia O'Donoghue, Cathy Nock, Sy Praseuthsouk and Stephan Williams; and postgraduate students working on Riversleigh fossil materials who have generously shared their understanding including Bernie Cooke, Jeanette Muirhead, Paul Willis and Anita Van der Meer. Particular thanks are owed to Sue and Jim Lavarack who spent many years slogging to and from Terrace Site as leaders of the 'Terracists'.

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PRISCILEO ROSKELLYAE SP. NOV. (THYLACOLEONIDAE, MARSUPIALIA) FROM THE OLIGOCENE-MIOCENE OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

ANNA GILLESPIE

Gillespie, A., 1997 06 30. *Priscileo roskellyae* sp. nov. (Thylacoleonidae, Marsupialia) from the Oligocene-Miocene of Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 321-327. Brisbane. ISSN 0079-8835.

Upper dentition of the marsupial lion *Priscileo roskellyae* sp. nov. from the Upper Site Local Fauna of Riversleigh provides the first detailed information about upper dentition of the genus. The upper adult dental formula is I1-3, C1, P1-3, M1-4. This species is smaller than *P. pitikantensis* and is the most plesiomorphic thylacoleonid. Relative to *Wakaleo*, P3 is less bowed and molars are square and have a metaconule at their posterior margin. □Thylacoleonidae, Wakaleoninae, *Priscileo*, Riversleigh, Oligocene, Miocene.

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The marsupial lion genus *Priscileo* Rauscher, 1987 contains only *P. pitikantensis* Rauscher, 1987, from the late Oligocene Ngapakaldi Local Fauna, S. Aust which is known only from a maxillary fragment, a few teeth, and a number of post cranial elements. Additional *Priscileo* material has been recovered from the Oligocene-Miocene of Riversleigh, northwestern Queensland. This material includes a near complete skull from the Upper Site Local Fauna representing *Priscileo roskellyae* sp. nov.

Dental terminology for molars and the last premolar follows Lockett (1993) who has shown that a molariform dP3 (M1 of Archer, 1978) in marsupials is replaced by P3. Accordingly, the remaining molars represent M1-4. However, homology of the other premolars follows Flower (1867). Material is housed in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra (CPC), Northern Territory Museum (NTM), Queensland Museum (QMF), South Australian Museum (SAMP), Museum of Palaeontology, University of California, Berkeley (UCMPB).

SYSTEMATICS

Superorder MARSUPIALIA Illiger, 1811
Order DIPROTODONTIA Owen, 1866
Family THYLACOLEONIDAE Gill, 1872

Priscileo Rauscher, 1987

TYPE SPECIES. *Priscileo pitikantensis* Rauscher, 1987.

DIAGNOSIS. Small; P3 length usually less than 12mm; M1 and M2 relatively square in basal

outline, with a posterolingual metaconule; anterior root of the zygomatic arch projecting anterolaterally dorsal to M2-3.

***Priscileo roskellyae* sp. nov.**
(Figs 1-3)

MATERIAL. Holotype QMF23453, a skull with left and right P3, M1-2, alveoli for left and right I2-3, C1, P1-2, M3-4, and partial alveoli for the left and right I1 from early Miocene Upper Site, Godthelp Hill, Riversleigh.

ETYMOLOGY. For the former Australian Minister of Arts, Sport, the Environment, Tourism and Territories, the Hon. Ros Kelly, who provided significant support for the Riversleigh Project.

DIAGNOSIS (by comparison with the type and only other species). Smaller; P3 approximately 2/3 as long; metaconule on M1 and M2; alveolus of P1 closer to the P2 alveolus than to the canine alveolus; lingual root on M1 smaller, not intruding as far medially into the palate.

DESCRIPTION. Upper dentition. Formula I1-3, C1, P1-3, M1-4. Alveoli for I1 large and incomplete. Alveolus for I2 smallest of incisor alveoli. Alveolus for C1 ovoid, larger than alveolus for I3, smaller than that for I1. Canine alveolus closer to I3 alveolus than to P1 alveolus. Two small alveoli for two single-rooted premolars between the canine and P3. C1 and P1 alveoli separated by an approximately 3 mm. P2 alveolus close behind that for P1, abutting the anterior base of P3.

P3. As in *Wakaleo* but 25-66% smaller. Posterior portion only slightly broader than the anterior

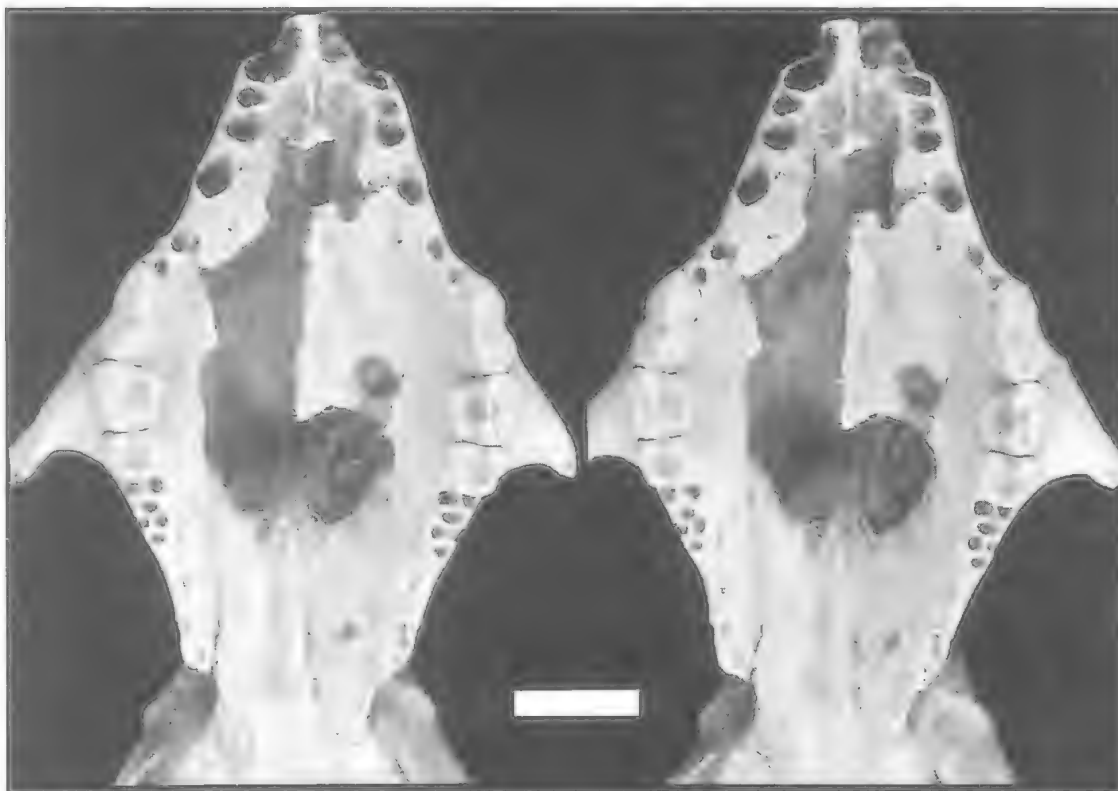


FIG. 1. *Priscileo roskellyae* sp. nov., holotype, QMF23453, partial skull, from Upper Site, Godthelp Hill, Riversleigh. Ventral view stereopair, showing upper dentition.

portion (unlike *Wakaleo* where the posterior is much broader). Longitudinal blade slightly inwardly-curved in contrast to the distinctive inwardly-curved blade of most *Wakaleo*. Relatively uniform width with gently curved longitudinal blade giving P3 rectangular shape. Longitudinal blade running between 2 major cusps. In buccal view, the shearing blade of P3 W-shaped, the longitudinal blade forming the rise in the middle, and the anterior and posterior blades ascending from the major cusps at each end. The anterior cusp is slightly higher than the posterior (as in *W. alcootaensis*). In *W. vanderleueri* the cusps are approximately equal in height. Three vertical blades, one anterior, one lingual, and one buccal, ascending from the anterior cusp to the base of the crown. Anterior blade curving lingually as it ascends, bending slightly posteriorly before merging with the base of the crown. Lingual curvature of blade producing a small vertical lip towards the base of the blade. Similar lip in some Riversleigh *Wakaleo*. Posterior to this blade lingual face of the crown curving concavely forming an anterolingual basin. Lingual blade

curving slightly anteriorly as it ascends and merges with the base of the crown. Many *T. carnifex* and *T. crassidentatus* also with lingual blade in contrast to *W. alcootaensis* and *W. vanderleueri* in which it is absent. Posterior to the lingual blade the lingual flank of P3 forming a sharp depression extending from the base to the crown. Lingual flank following the curve of the posterior root, curving convexly to the posterior border. Buccal blade of the anterior cusp ascending in a slight posterior direction, merging with the crown midway up the tooth. Short buccal blade also ascending from the posterior cusp, merging with the crown midway up the tooth, not as prominent as the anterior buccal blade. Similar anterior and posterior buccal blades in *Wakaleo*. Posterior blade running posterolaterally from the posterior cusp to the posterior margin of the tooth, an extension of the longitudinal blade, contiguous with the preparacrista of M1, in P3 of *Wakaleo* but absent in *Thylacoleo*. Short oblique blade at termination of posterior blade at the posterior margin of P3, ascending anterolaterally on the buccal flank, merging midway with the base of

TABLE 1. Dimensions of upper cheek teeth of species of *Priscileo* and *Wakaleo*. Data from Clemens & Plane (1974), Archer & Rich (1982), Rauscher (1987) and Murray & Megirian (1990). Measurements for *P. pitikantensis* (except P3) were taken from from a caste of UCMP88448. a=alveolus measurement.

	Length (mm)					
	P3	M1	M2	M3	M4	P3/M1
<i>P. roskellyae</i>						
QMF23453	8.2	5.8	4.3	3.3a	2.9a	1.41
<i>P. pitikantensis</i>						
UCMP88448	11.0a	6.5a	5.3	3.7a	3.5a	1.69
<i>W. alcootaensis</i>						
NTM P1	23.3	14.7	7.2	?	-	1.58
<i>W. vanderleuerei</i>						
CPC26604	17.9	11.2	7.0	5.0	-	1.59
Riversleigh <i>Wakaleo</i>						
QMF24680	12.9a	8.9a	6.3	4.9a	4.3a	1.44
QMF23446	12.6	9.6	6.0	5.2	-	1.31
QMF23443	12.2	9.4	6.0	4.5	3.5a	1.30

the crown, lacking in *Thylacoleo* and *W. alcootaensis*. *W. vanderleuerei* with a small blade in a similar position, differing by commencing a short distance before the end of the posterior blade, more vertically oriented. On the buccal flank of P3, a broad valley running between the anterior and posterior buccal blades, much broader, in *Wakaleo*.

Molars. Left and right M1 and M2 relatively unworn. Alveoli for M3 and M4 indicating 3 roots for each; 2 equal anterior roots, with slightly larger posterior one. In *Wakaleo vanderleuerei* anterior roots of M3 larger. Molar gradient steep, similar to *P. pitikantensis* and *Wakaleo*. M1 and M2 square, unlike the triangular molars in *Wakaleo*. Molar morphology similar to *Wakaleo*. M1 wider anteriorly than posteriorly. Paracone highest cusp. Small blade ascending anteriorly from the paracone to the anterior edge, joining stylar cusp B, contiguous with blade ascending from the posterior cusp of P3. Postparaacrista running posteriorly, meeting the ascending premetacrista, forming a notch midway along the straight centrocrista. Metacone well-developed. Postmetacrista ascending posteriorly from the metacone to the posterior margin of M1. Buttressing the steep lingual face of the paracone a short crescent-shaped preparaconulecrista straightening medially, terminating at a paraconule. Short postparaconulecrista running posteriorly into the

trigon basin. *W. vanderleuerei* and Riversleigh *Wakaleo* with much straighter and longer blade ascending lingually from the paracone. Preprotocrista arising from the anterior edge of the trigon basin medial to the paraconule, running posteromedially to the protocone. From the protocone a postprotocrista running posteriorly to a metaconule. Postmetaconulecrista curving posterolaterally from the metaconule, ascending to merge with the posterior margin of the postmetacrista. Short crescent-shaped ridge ascending lingual face of metacone, terminating midway between metacone and metaconule. M1 of *W. vanderleuerei* and Riversleigh *Wakaleo* with similar ridge. Blades joining the 4 major cusps forming margins of a deep, square trigon basin. Within the basin, fine enamel crenulations radiate outwards. Similar crenulated trigon basins occur in *Wakaleo* and *T. crassidentatus*. Buccal flank of M1, especially anteriorly, swollen resulting in a broad base for the stylar shelf. A stylar basin running from the posterobuccal face of the paracone to the posterobuccal margin of the metacone, becoming shallower posteriorly. Lateral wall of the basin lined with small vertical ridges.

M2. M2 smaller than M1, lacking the distinctive broad stylar shelf and basin. Paracone highest cusp, more lateral than in M1. Short, semicircular preparaacrista running anteromedially from the paracone. Small ridge buttressing lingual base of the paracone. Medial to this ridge a preprotocrista arising, running posteromedially to the protocone. Protocone prominent, more anteriorly placed than in M1. Protocone lingually bulbous as in *P. pitikantensis* and *Wakaleo*. A narrow anterior shelf running from the base of the preparaacrista to the protocone. Postprotocrista running posterobuccally to a gently-rounded, posterior metaconule, producing squaring of the lingual outline. No metaconule on M2 of *P. pitikantensis* but could be lost by damage to rear portion of the tooth. Short postmetaconulecrista running posterolaterally, merging with the posterior margin of the tooth. Metacone rounded and more posteriorly situated than in M1, with lingual blade running medially, connecting with a small blade running laterally from the metaconule, forming anterior border of a small, oval, basin at the posterior. Postparaacrista running posterolaterally to the buccal margin of the stylar shelf, converging with anterolaterally orientated premetacrista. Deep, square, trigon basin between the major cusps with fine enamel crenula-

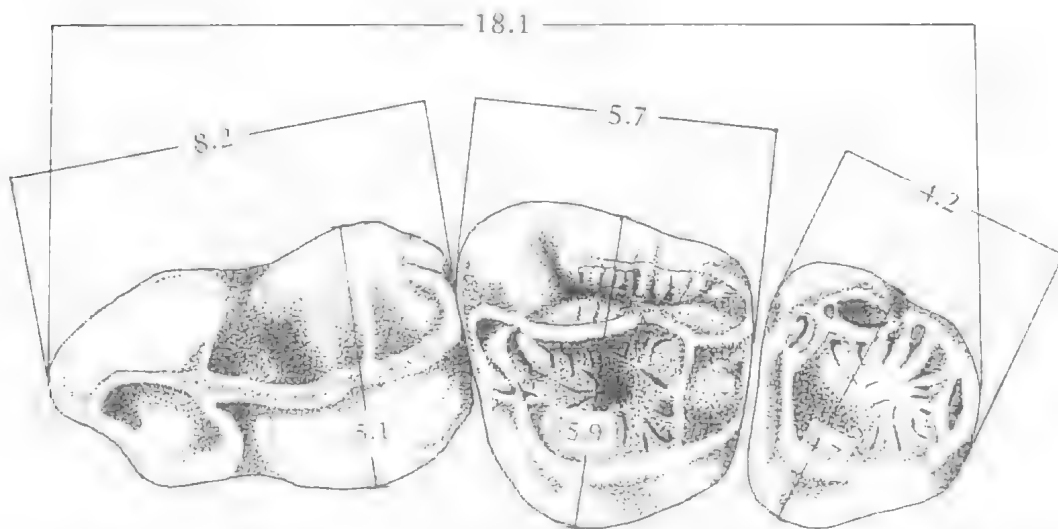


FIG. 2. *Priscileo roskellyae* sp. nov., holotype, QMF23453, measurements (mm) of left tooth row. P³ on left, M¹ and M².

tions concentrated on the lateral and posterior walls. Crenulated basins in M2 of *P. pitikantensis* and *Wakaleo*. On the buccal margin of M2 a small, elongate, styler basin parallel to the postparacrista, terminating midway between the paracone and metacone. Similar basin in Riversleigh *Wakaleo*, difficult to discern in the heavily worn M2 of *W. vanderleueri*.

COMPARISON. *P. roskellyae* differs from all species of *Wakaleo* in: being smaller; the P3 of *P. roskellyae* is approximately 1/3 length of P3 of *W. alchootaensis*, 1/2 the length of P3 of *W. vanderleueri*, and 2/3 the length of P3s of Riversleigh *Wakaleo*; having a lingual crest ascend from the anterior cusp of P3; having the shearing blade of P3 straighter; having the posterior root of P3 only slightly enlarged; having the posterior half of P3 relatively square in basal outline; having M1 and M2 relatively square in basal outline. *P. roskellyae* differs from *Thylacoleo* in: being smaller; P3 being approximately 1/3 length of P3 of *T. hilli* and 1/6 length of P3 of *T. carnifex*; having M3+4; having M1+2 relatively square in basal outline.

DISCUSSION

The diagnosis of *Priscileo* is amended to include *P. roskellyae*. Rauscher (1987) distinguished *Priscileo* from other thylacoleonids by M4, a P3/M1 length ratio less than 1.70, and M2 with a

crenulate, anteroposteriorly broad trigon basin. Some of the new Riversleigh *Wakaleo* specimens have these features. Two *Wakaleo* specimens have an M4 (Table 1), and most have a relatively broad crenulated basin on M2. All species of *Wakaleo* have a P3/M1 ratio of less than 1.70. The value for *P. roskellyae* (1.41) falls midway within this range.

Rauscher (1987) distinguished *Priscileo* from *Wakaleo* by the loss of P1 or 2 and M4 in the latter. Although some new Riversleigh *Wakaleo* specimens have these teeth, the plesiomorphic features of *P. roskellyae* exhibits (significantly smaller size, square molar shape, metaconule and relatively straight cutting blade on P3) require generic distinction. *P. pitikantensis* and *P. roskellyae* share generic features of dental dimensions, shape of M2 and position of the anterior base of the zygomatic arch. Specific distinction of *P. roskellyae* is based on the size difference between these two species, *P. pitikantensis* being 33% larger.

INTRAFAMILIAL RELATIONSHIPS

Rauscher (1987) found no synapomorphies uniting *Priscileo* and *Wakaleo*, or uniting *Priscileo* and *Thylacoleo*. Analysis of *Priscileo* and *Thylacoleo* included comparison of postcranial material and for a number of character-states. *Thylacoleo* exhibited the plesiomorphic condition while *Priscileo* was derived. Rauscher con-

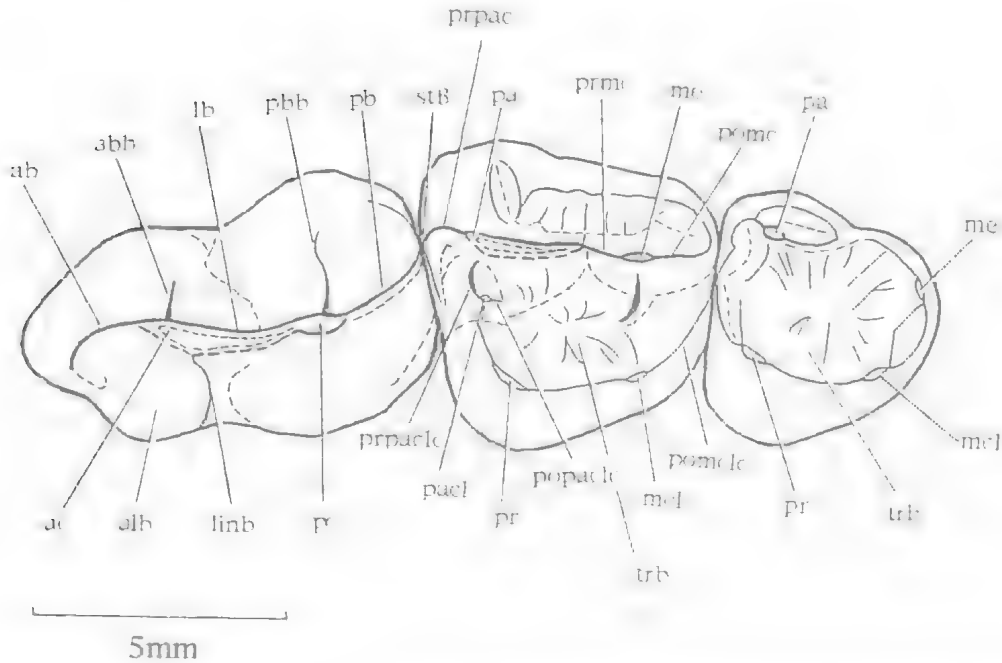


FIG. 3. *Priscileo roskellyae* sp. nov., holotype, QMF23453. left cheek dentition. lb=longitudinal blade; ab=anterior blade; pb=posterior blade; ac=anterior cusp; pc=posterior cusp; abb=anterior buccal blade; linb=lingual blade; pbb=posterior buccal blade; alb=anterior lingual basin; pa=paracone; pael=paraconule; prpac=preparaerista; popac=postparaerista; prpael=preparaconulecrista; popael=postparaconulecrista; pr=protocone; mel=metaconule; pomec=postmetaconulecrista; me=metacone; pome=postmetaerista; prme=premetaerista; stB=stylar cusp B; trb=trigone basin.

cluded that *Thylacoleo*'s primitive features were secondarily derived and not a retained plesiomorphic condition. Because *Wakaleo* and *Thylacoleo* share the synapomorphy of loss of M4, Rauscher (1987) considered them to be sister groups. *Priscileo* was regarded as the sister group of a *Wakaleo*/*Thylacoleo* clade.

Rauscher (1987) suggested that loss of the metaconule could be a diagnostic feature for the Thylacoleonidae based on the tritubercular upper molars of *Wakaleo* and *Priscileo* and the secondarily quadritubercular M1 of *Thylacoleo*. However, M1 and M2 of *P. roskellyae* have a metaconule and are basically square in outline. The metaconule on these molars, especially on M2, is posteriorly positioned and its seeming absence from M2 of *P. pitikantensis* may be a result of damage which is evident at the rear margin of this tooth. Consequently, loss of the metaconule can no longer be considered a synapomorphy for the family.

Murray et al. (1987) placed *Wakaleo* and *Thylacoleo* in separate subfamilies; the Wakaleoninae includes *Wakaleo*; and the

Thylacoleoninae which includes *Thylacoleo* and possibly *Priscileo*. Wakaleonines were regarded to differ from thylacoleonines in absence of P1 and formation of a tympanic wing composed of alisphenoid and squamosal contributions. Features distinguishing thylacoleonines from wakaleonines include P1, squamosal contribution to the tympanic wing and frontal-squamosal contact on the lateral cranial wall. The new thylacoleonid specimens from Riversleigh indicate that, in terms of dental morphology, *Priscileo* exhibits no features that prevent it from being ancestral to *Wakaleo* and *Thylacoleo*. The dental features of *Priscileo*, including small P3 and molar size, square (nearly bunodont) molar shape, metaconule, and full premolar and molar complement are almost certainly plesiomorphic features within the family.

However, these same features clarify some questions about relationships of the family with the Order Diprotodontia. It was once commonly believed that thylacoleonids evolved from a phalangerid-like diprotodontian which had quadritubercular upper molars including a hyper-

trophied metaconule (Kretz, 1872; Broom, 1898; Bensley, 1903; Ride, 1964; Archer, 1976). Archer & Rich (1982) hypothesised that the tritubercular shape of the molars of *W. alcocki* were secondarily derived from an ancestral quadritubercular shape through suppression of the metaconule. It has been suggested that the triangular molars of *Wakaleo* are plesiomorphic for the family (Murray et al., 1987). The primitive dental features of *P. roskellyae*, especially the metaconule and square molar shape, provide support for Archer & Rich (1982).

Priscileo and *Wakaleo* have been collected from Riversleigh's System B sites indicating overlapping of early Miocene thylacoleonid lineages. Temporal overlapping of species of *Thylacoleo* (*T. crassidentatus* and *T. hilli*) also occurred in the early Pliocene (Archer & Dawson, 1982). In each case there was a distinct size difference in the lineages involved. In terms of P3 length, System B specimens of *Wakaleo* are approximately 1.5 times larger than *P. roskellyae*. Similarly, P3 of *T. crassidentatus* is twice the length of that tooth in *T. hilli* (Pledge, 1977). It is possible that size differences of this magnitude among sympatric thylacoleonids were an important factor in reducing competition. Morphological studies of the limbs of *P. pitikantensis* suggest it was arboreal (Rauscher, 1987). *Wakaleo*, being larger and no doubt heavier, may have been more terrestrial. Murray & Megirian (1990) also intimated a terrestrial existence for *Wakaleo* based on the wrist joint and heavily-worn dentition which they consider may indicate a scavenging mode of life.

ACKNOWLEDGEMENTS

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ZYZOMYS RACKHAMI SP. NOV. (RODENTIA, MURIDAE) A ROCKRAT FROM
PLIOCENE RACKHAM'S ROOST SITE, RIVERSLEIGH,
NORTHWESTERN QUEENSLAND

H. GODTHELP

Godthelp, H., 1997:06:30. *Zyzomys rackhami* sp. nov. (Rodentia, Muridae) a rockrat from Pliocene Rackham's Roost Site, Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 329-333. Brisbane. ISSN 0079-8835.

Zyzomys rackhami sp. nov. from the Pliocene Rackham's Roost Site, Riversleigh, northwestern Queensland is the first fossil member of this genus and only the second Tertiary murid described from Australia. It is known from many hundreds of dental fragments recovered as a part of an ancient megadermatid roosting cave. It appears to be the most plesiomorphic member of the genus and is part of a diverse suite of extinct murids from this site. *M Rodentia, Muridae, Zyzomys, Pliocene, Riversleigh.*

H. Godthelp, School of Biological Science, University of New South Wales, New South Wales 2052, Australia; 4 November 1996.

The murid genus *Zyzomys* contains 5 living species which are restricted to tropical Australia. *Zyzomys* has been placed in the tribe Conilurini (Baverstock, 1984) and is an 'Old Endemic' sensu Ride (1970) or an 'Older Immigrant' of Tate (1951). Along with *Mesembriomys* and *Conilurus*, *Zyzomys* comprises a group of taxa unified by a number of cranio-dental characters, phallic morphology (Lidicker, 1987) and chromosomes (Baverstock et al., 1981).

Dental nomenclature follows Musser (1981). Measurements are in millimetres. Unless otherwise stated material is housed in the Queensland Museum (QMF).

SYSTEMATICS

Order RODENTIA Bowdich, 1821
Suborder MYOMORPHIA Brandt, 1855
Infraorder MYODONTA Schaub, 1958
Superfamily MUROIDEA Miller & Gidley,
1918
Family MURIDAE Gray, 1821
Subfamily MURINAE Gray, 1821

Zyzomys Thomas, 1909

Zyzomys rackhami sp. nov.
(Figs 1-2, Table 1)

MATERIAL. Holotype QMF10818, partial left maxillary with M¹⁻³.

ETYMOLOGY. For Alan Rackham, the discoverer of the Rackham's Roost Site. Paratype QMF10819, left maxillary fragment with M¹ and zygomatic plate. Other material QMF23365, partial left maxillary with

M¹⁻²; QMF10821, partial right maxillary with M¹⁻³; QMF23325, partial right maxillary M¹⁻³; QMF10819, left M¹; QMF24001, partial left maxillary with M¹⁻²; QMF24004, partial left maxillary with M¹⁻²; QMF24002, right M¹; QMF24003, right M¹.

All from Rackham's Roost Site (19°02'09" S, 138°41'60" E) at Riversleigh, NW Queensland. The site represents the remnants of an ancient cave which has largely eroded away leaving the indurated floor sediments exposed. The sediments of the floor contain myriad bones and teeth, mostly fragmented, which are interpreted to be megadermatid (*Macroderma* and *Megaderma* spp.) prey remains (Godthelp, 1988; Hand, 1994). Its age is Pliocene on the basis of a macropodid similar to *Protemnodon snewini* Bartholamai (1978) which species occurs in the early to middle Pliocene Bluff Downs Local Fauna (Archer & Wade, 1976; Bartholamai, 1978).

DIAGNOSIS. *Zyzomys rackhami* differs from other species of the genus by the following combination of characters: Relatively well-developed series of cusps (T3,6,9) particularly T3, relatively small proportions of the lingual series of cusps (1,3,7), reduced molar gradient, frequent T1bis; tooth row short and narrow.

DESCRIPTION. Small to medium-sized dental arcade arcuate and concave lingually with the internal edge of M³ as the most lingual point of the tooth row. M¹ longer than M². M³ small and relatively reduced. All cusps and cusp complexes with marked posteriorly inclined slant except in M³ with cusps nearly vertical. Molar overlap minimal.

M¹. Relatively long and narrow often with a prominent anterior cingulum which forms a semi-



FIG. 1. *Zyzomys rackhami* sp. nov., Rackham's Roost Site, holotype, QMF10818, SEM (stereo pair).

circle around the T2,3 complex in the holotype. Anterior cingulum with a series of small but apparently occlusally functional accessory cusps randomly positioned. T1 elliptical with its long axis obliquely inclined to the axis of the T2,3 complex, directed to the rear of the tooth and positioned posterior to the base line of the T2,3 complex. T1 joined to the T2,3 complex only in extreme stages of wear and in some specimens via a variably sized and shaped T1bis.

T1bis with its long axis inclined obliquely to the axis of the T8,9 complex but in reverse to the angles of T1 and T4 and as such is directed forwards. T7 and T4 in very close proximity, forming a single complex after moderate to extreme wear. T8 large, with a nearly circular occlusal surface. T9 barely discernible, incorporated into the T8,9 complex at the onset of wear. Slight furrow in the anterior surface of the T8,9 complex marking the anterolingual edge of T9 (would remain even

structure in the holotype small, becoming more prominent with increased wear. T2 large and arcuate anteriorly with a straight posterior edge, more than half the width of the anterior portion of the tooth. T2 joined to T3 at its buccal edge. T3 small and circular, with its posterior third behind the posterior edge of T2, almost entirely incorporated into the T2 complex with wear. T4 elliptical with its long axis inclined obliquely to the axis of the T5,6 complex and directed posteriorly. T4 occlusal surface approximating T1 in size and shape if unworn, larger in worn specimens, joined to T5 in early stages of wear, nearly wholly incorporated in older individuals. T5 large, with a subangular arcuate anterior edge, with posteriorly concave posterior edge, with a smaller occlusal surface area than T2. T6 strongly attached to T5 even in early stages of wear, with junction of these two cusps marked by a cleft on the occlusal surface that continues anteriorly and ventrally as a furrow in the enamel indicating that the distinction between T5 and T6 is never lost. T6 circular, smaller than T3, approximately half of T6 behind the posterior edge of T5. T7 larger than T4, elliptical,



FIG. 2. *Zyzomys rackhami* sp. nov., paratype, QMF10821, SEM showing zygomatic plate.

with moderate wear). Posterior cingulum (z) absent.

M², T1 large, tear-shaped, with a long axis obliquely inclined to the anterior edge of the tooth and directed posteriorly. T2 and T3 absent. T4 of moderate size, elliptical, posterior to the dominant T5. T4 joined to T5 in very early stages of wear. T5 subtriangular in occlusal outline, with its anterior most edge of the enamel boundary contacting the posterior edge of M¹ in extreme wear. T6 small, circular, joined to T5 with moderate wear. As in the T6 structure of M¹, the connection associated with a well-defined furrow, this cusp always retaining its identity. T7 an elliptical cusp of moderate size, with its axis running almost parallel to the main axis of the tooth, not observed to merge with the T8,9 complex in M² even with extreme wear. T8 large, nearly circular, with distal edge extending well beyond the distal edge of T7, giving the posterior region of the tooth an arcuate shape. T9 lost, with a remnant of the furrow that marked the position of the lingual side of the cusp.

M³, T1 small, almost circular. T2 and T3 absent. T4 small, tear-shaped, joined to T5 after

little wear, with an axis directed across the width of the tooth. T5 small, subtriangular, displaced toward the buccal edge of the tooth. T6 absent, with only a poorly defined remnant of the lingual furrow forming a weak buccal cingulum at the anterior edge. T7 moderate in size, shaped as a bisected semi-circle. T8 a mirror image of T7, with the 2 cusps joined in early wear. T9 absent.

M¹ with 4 roots, 3 well-developed, fourth small and probably reduced; anterior root large, directed forwards, exposed occlusally; medio-lingual root long, narrow, positioned under T1 and the anterior edge of T4; medio-buccal root a remnant of a more substantial root, with an alveolus for this root on all specimens examined even though there is not always a root. Posterior root large, nearly as wide as the tooth at its origin, directed towards the buccal edge of the maxillary. M² with 3 roots; anterolingual and anterobuccal roots of equal size, together below the anterior margin of the tooth; posterior root wide, running obliquely with respect to the anterior roots, with lingual extremity its most posterior point. M³ with 3 roots of equal size, forming a triangle with a root at each apex. As in M² there are 2 anterior roots (buccal and lingual).

Occlusal surface of the tooth row concave, with the highest points being the anterior third of M¹ and the M³. Anterior palatal vacuity extending distally as far the anterior edge of M¹. Attachment node for the origin of the superficial masseter large and well defined. Anterior edge of the node aligned with the anterior edge of the zygomatic plate and just behind the maxillary/premaxillary suture. Zygomatic with anterior edge rising vertically and straight, of moderate width, with one nutrient foramen distally near its base.

COMPARISON. Although the nearest species in size *Z. argurus*, *Z. rackhami* is more similar to *Z. pedunculatus* because of the relatively cuspidate nature of the teeth, the development of the buccal series of cusps and the relatively unreduced appearance of M³. These similarities are probably simplesiomorphies. A nutrient foramen is found anterior to the tooth row in all species with the exception of *Z. rackhami* and *Z. maini*, in which the foramen is on the zygomatic plate. Unlike *Z. maini* however *Z. rackhami* has a longitudinal palatal crest as in all other species of *Zyzomys*.

Zyzomys rackhami differs from *Pseudomys*,

TABLE 1 Measurements (mm) of *Zyzomys rackhami* sp. nov. L=length; W=width.

SPEC. NO.	M ¹⁻³ L	M ¹⁻² L	M ¹	
			L	W
QMF10818	5.3	4.3	2.6	1.5
QMF10821	5.6	4.4	2.7	1.5
QMF23325	5.3	4.3	2.7	1.7
QMF10819	-	-	2.7	1.7
QMF23365	-	4.2	2.6	1.5
QMF24001	-	4.3	2.5	1.6
QMF24002	-	-	2.5	1.5
QMF24003	-	-	2.7	1.5
QMF24004	-	4.2	2.6	1.5
QMF30065	-	4.2	2.6	1.5
QMF30063	-	4.2	2.6	1.5
QMF30062	-	-	2.6	1.5
QMF24503	-	4.2	2.6	1.5
QMF10810	-	-	2.7	1.6
QMF30268	-	4.3	2.6	1.5
QMF30265	-	4.3	2.6	1.5

Mastacomys, *Leporillus*, *Notomys*, *Leggadina*, *Rattus*, *Melomys* and *Uromys* in having a well-developed T7. *Z. rackhami* is distinguished from *Pogonomys* by the lack of a posterior cingulum (α) and by smaller and less pronounced buccal cusps (T3,6,9). *Z. rackhami* differs from *Hydromys* and *Xeromys* in having 3 upper molars. *Z. rackhami* differs from *Conilurus* in having a well-developed T3 and T1 isolated from and distal to the T2,3 complex. *Z. rackhami* is removed from *Mesembriomys* by retaining a T9 on M¹, close proximity of T7 to the T8,9 complex, reduced molar overlap and less cuspidate nature of the molars.

DISCUSSION. *Zyzomys rackhami* is the most abundant (mainly isolated molars) rodent in the Rackham's Roost deposit but only a few maxillary fragments are known. Skulls apparently break up more readily than other murids from the deposit.

Lower jaws of rodents are uncommon in the deposit and not well preserved. No elements of the lower dentition of *Z. rackhami* have been identified. There is apparently some taphonomic process limiting the number of dentaries preserved. This might be caused by some aspect of the feeding behaviour of *Macroderma gigas*, the presumed predator, or by some physical process of sorting within the original cave system. In the latter case it is possible that we might find a

concentration of these elements elsewhere in the deposit. Lower jaws and teeth of other mammal groups (i.e., marsupials, bats) found in the deposit appear to be as abundant as their upper counterparts.

Z. rackhami is the only species of *Zyzomys* recovered from the Rackham's Roost Local Fauna and is represented by hundreds of specimens. This is in contrast to modern and Pleistocene faunas, in which there are usually at least 2 species present and sometimes, as in the Nourlangie Rock area, N.T., 3 (Kitchener (1989) reported only 2 but the author has sighted 2 specimens of *Z. woodwardi*, CM7200 and CM7200, from the area.) Areas on the east coast where only *Z. argurus* is now found appear to have lost a second species, *Z. woodwardi*, only recently, as is the case in the Chillagoe area. *Z. pedunculatus* occurs in surficial cave deposits at Cape Range, Western Australia along with *Z. argurus* which is still extant locally. In the Riversleigh area *Z. argurus* has been trapped and *Z. woodwardi* has been recovered from Recent owl pellet deposits along the Gregory River. Both *Z. argurus* and *Z. woodwardi* have been recovered from *Macroderma gigas* prey remains in Carrington's Cave on Riversleigh Station. The deposits in Carrington's Cave are as yet undated but appear to range from Recent to Pleistocene. The presence of both species in these deposits indicates that *M. gigas* is capable of taking the relatively larger *Z. woodwardi* as prey. Pliocene *M. gigas* from Rackham's Roost were not different in size (Hand, 1994) from the modern population and prey size would seem to be an unlikely explanation for the absence of a second *Zyzomys* in the Rackham's Roost deposit.

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NEW MIOCENE LEAF-NOSED BATS (MICROCHIROPTERA: HIPPOSIDERIDAE) FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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Hand, S.J. 1997 06 30: New Miocene leaf-nosed bats (Microchiroptera: Hipposideridae) from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 335-349, Brisbane. ISSN 0079-8835.

Two new Australian Tertiary hipposiderids are described on the basis of skull and dental material recovered from Bitesantennary Site, a Miocene cave-fill on the Site D Plateau, Riversleigh, northwestern Queensland. The new species are closely related to *Hipposideros* (*Brachhipposideros*) *nooraleebus* Sigé, Hand & Archer from Riversleigh's Microsite, and the living northern Australian *Rhinonictis aurantius* (Gray). One species is referred to *Rhinonictis*, the other tentatively referred to *Brachhipposideros*. The subgenus *Brachhipposideros* Sigé is raised to generic rank to better reflect relationships of its species.

□ *Miocene, Riversleigh, hipposiderids, leaf-nosed bats.*

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Bitesantennary Site, in early Miocene (Archer et al., 1989; Creaser, 1997) freshwater limestone on the NE edge of the Site D Plateau at Riversleigh (Hand et al., 1989; Archer et al., 1989, 1994) covers approximately 150m² and contains thousands of bat skulls, limb bones and snails. Almost all are complete, suggesting fossilisation at or very near the point of accumulation. This deposit is interpreted as a cave-fill (Hand et al., 1989) and contains at least 11 microchiropteran species - 10 hipposiderids and a megadermatid. At least 4 of the Bitesantennary hipposiderids are known from many hundreds of partial and complete skulls. Two of the hipposiderids, which are morphologically similar to Microsite's *Brachhipposideros nooraleebus* Sigé et al., 1982, are described and their phylogenetic relationships and palaeoecology are discussed.

Skull terminology follows Hand (1993, 1995); dental terminology follows Sigé et al. (1982). Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1989, 1994; Creaser this volume). The prefix QMF refers to specimens held in the fossil collections of the Queensland Museum, Brisbane.

SYSTEMATICS

Suborder MICROCHIROPTERA Dobson, 1875
Superfamily RHINOLOPHOIDEA Weber,
1928
Family HIPPOSIDERIDAE Miller, 1907

Rhinonictis Gray, 1847

Rhinonictis tedfordi sp. nov. (Figs 1-2, Table 1)

MATERIAL. Holotype QMF22910, partial skull with RM¹, LM¹. Paratypes QMF22911, partial skull with RP¹-M¹ and LM²⁻³; QMF22912, maxillary fragment with RC¹-M¹; QMF22840, rostrum with LC¹-M¹; types from early Miocene (System B) Bitesantennary Site. Other material: Bitesantennary Site: QMF22831, QMF22841, QMF22842, QMF22845, QMF22854, QMF22859, QMF22865, QMF22871, QMF22890, QMF22891, QMF22893, QMF22909. White Hunter Site (System A): QMF22921, QMF22922. RV Site (System B): QMF22930, QMF22931, QMF22932, QMF22913. Upper Site (System B): QMF22914. White Hunter, RV and Upper Sites are about 2km SSW of the type locality.

ETYMOLOGY. For Richard Tedford, American Museum of Natural History who described the first Tertiary mammals from Riversleigh in 1967.

ASSOCIATED FAUNA AND TAPHONOMY. The cave-fill (Hand et al., 1989) at the type locality contains thousands of well preserved, almost complete bat skulls and limb bones, suggesting fossilisation at or near the point of accumulation. Contact between the fill and older cave wall have been identified. The deposit's many freshwater snails suggest that the depositional area was open to light and under water for some period during its history. A travertine floor, including a large stalagmite, has been found at the base of the deposit.

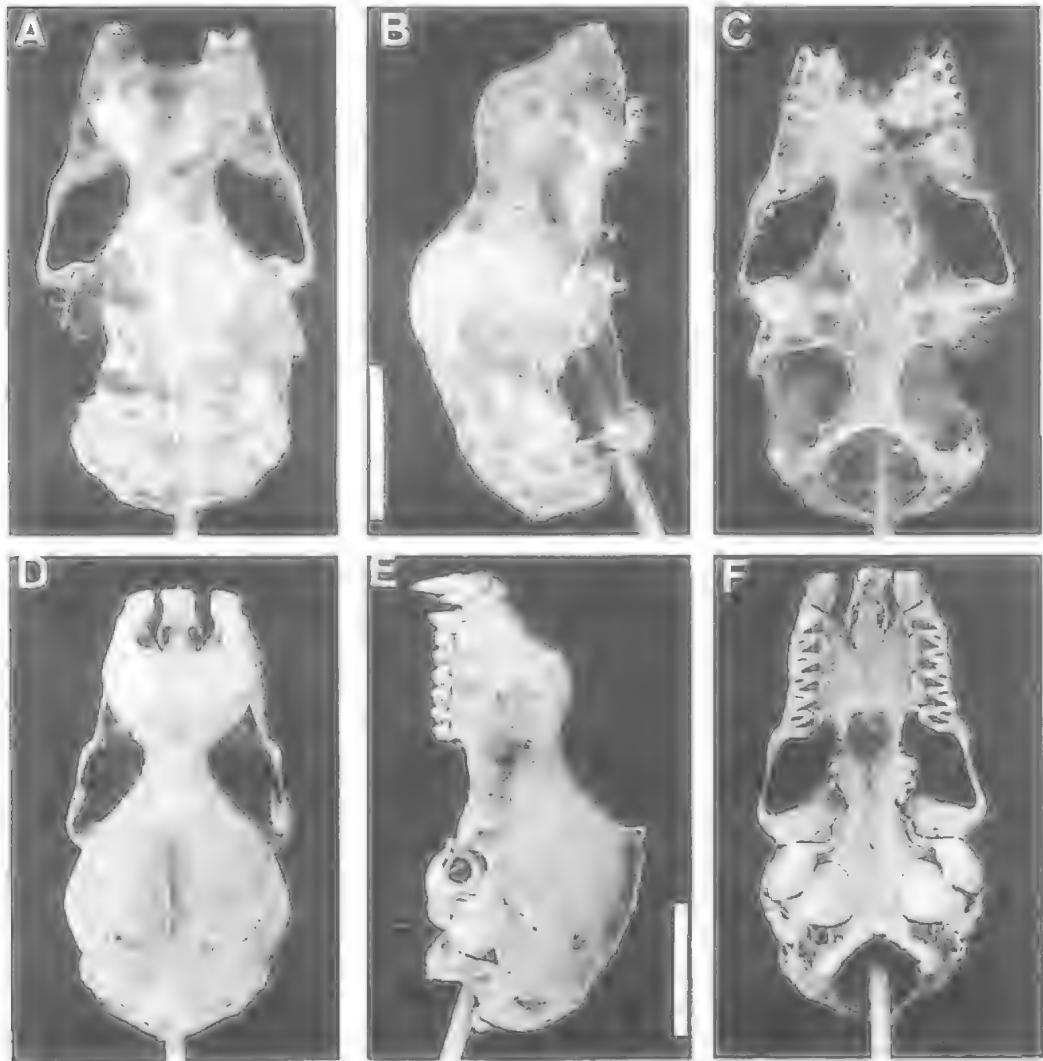


FIG. 1. A-C, *Rhinonictes tedfordi* sp. nov., QMF22910, holotype, from Bitesantennary Site, Riversleigh, northwestern Queensland. A, dorsal view; B, lateral view; C, ventral view. D-F, *Rhinonictes aurantius*. AR 15400, Klondyke Queens Mine, Marble Bar, Western Australia. D, dorsal view; E, lateral view; F, ventral view. Scale indicates 5 mm.

Bitesantennary Site contains *R. tedfordi*, ?*B. watsoni* and at least 8 other hipposiderids and a megadermatid with rarer frogs, lizards, a boid, a stork, swift, peramelids, a dasyurid and a bulungamayine macropodid (Archer et al., 1994).

In the complex lacustrine White Hunter, Upper and RV deposits the vertebrate faunas are much more diverse, with the Upper Local Fauna (Archer et al. 1994) one of Riversleigh's richest.

DESCRIPTION. In comparison to Miocene *B.*

nooraleebus Sigé et al., 1982 and Recent *Rhinonictes aurantius* (Gray, 1845).

Skull 10-20% smaller than *R. aurantius* and approximately same size as *B. nooraleebus* (braincase may be slightly longer in *R. tedfordi*). Proportions similar to *B. nooraleebus*: rostrum wide and long with respect to braincase, approximately 2/3 braincase length, 2/3 maximum (mastoid) width and twice interorbital width. Zygomatic width greater than mastoid width. Maximum height of the skull dorsal to the glenoid process as in *R. aurantius*. In dorsal view, poste-

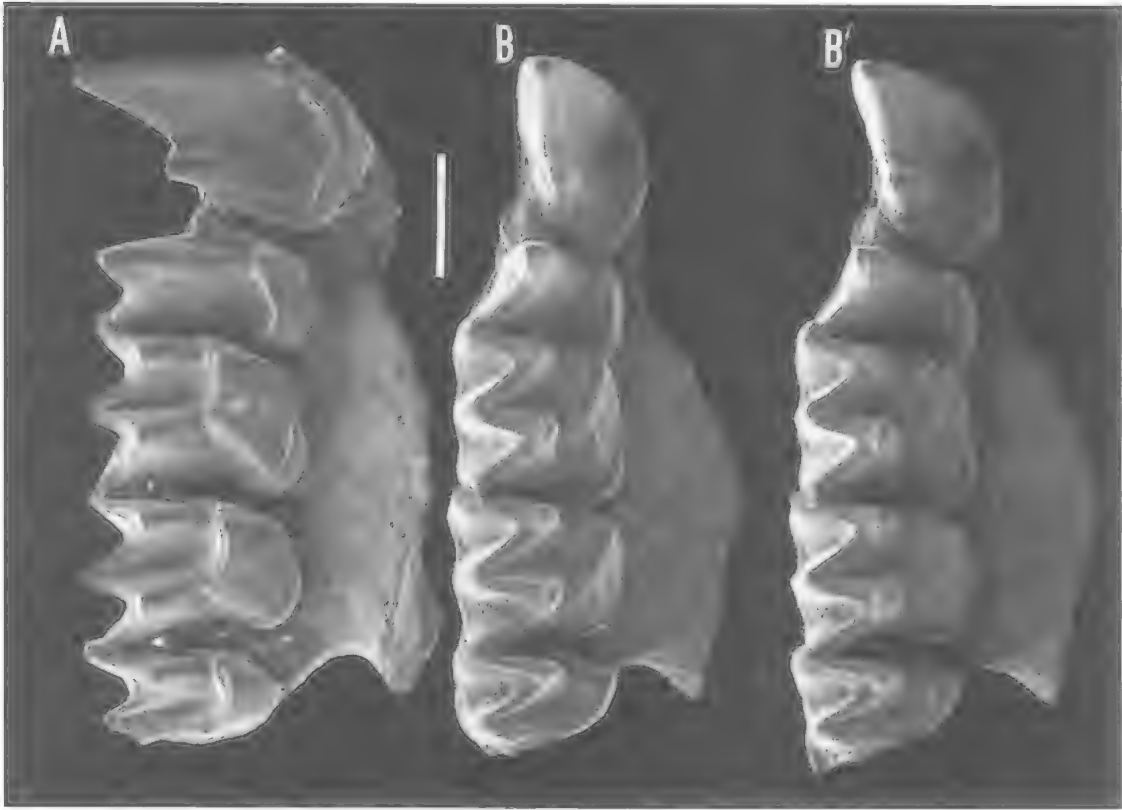


FIG. 2. *Rhinonicteris tedfordi* sp. nov., QMF22912, paratype, maxillary fragment with C^1 - M^3 , from Bitesantennary Site, Riversleigh, northwestern Queensland. A, oblique-occlusal view; B-B', occlusal view, stereopairs. Scale indicates 1 mm.

rior margin of the skull quadrate rather than rounded as in *R. aurantius* and *B. nooraleebus*.

Rostrum distinctly lower than the braincase, more so than in *B. nooraleebus* but less than in *R. aurantius*. Rostral inflations much more prominent than in *B. nooraleebus* and *R. aurantius*, mainly because of the very marked groove leading to a deep frontal depression delimited sharply by well-developed supraorbital ridges. *R. aurantius* with inflations better developed, with very little development of supraorbital ridges, with frontal depression and groove between rostral inflations more limited in depth and extent. Infraorbital foramen wholly above M^2 as in *B. nooraleebus*, but unlike *R. aurantius* (above M^{2-3}), larger and more rounded than in *B. nooraleebus*, smaller and slightly more elongated than in *R. aurantius*. Bar of bone forming its dorsal margin (anteorbital bar; e.g. Hill 1963) straighter and wider anterodorsally than in *R. aurantius* (being roughly the same thickness throughout), (In *R. aurantius* this bone curved, about 3 times as wide

posteroventrally as anterodorsally.), more curved than in *B. nooraleebus*, in which it is roughly the same thickness throughout and very straight. Zygoma (as in *B. nooraleebus* and *R. aurantius*) with an enlarged jugal projection occupying much of its length, as tall as the level of the lower insertion of the anteorbital bar, with slightly convex posterior margin, with its anterior edge posterodorsally directed (rather than vertically).

Sagittal crest well-developed (but see QMF22871), much better developed than in *B. nooraleebus* and different to *R. aurantius*, with maximal height anterior to the middle of the braincase level with the posterior zygomatic roots, not terminating as abruptly nor in a forwardly curving projection as in *R. aurantius*, extending further anteriorly onto the moderately constricted interorbital region, not joining the supraorbital ridges as distinctly as in *B. nooraleebus*, extending posteriorly to the lambdoidal crest, rather than attenuating in the interparietal region as in *R. aurantius*.

TABLE 1. Skull and dental measurements (mm) of type material. H=holotype; P=paratype; two measurements in parentheses in a column indicate (left) and (right), respectively.

	<i>Rhinonictis tedfordi</i>			<i>?Brachiposideros watsoni</i>		
	QMF 22910 (H)	QMF22911 (P)	QMF22912 (P)	QMF22915 (H)	QMF22828 (P)	QMF22916 (P)
Greatest skull length (dorsal)	15.0	15.4		14.4		
Rostral length	5.0	5.5		4.6	24.2	
Braincase length	10.0	9.9		9.6	10.1	
Rostral width (at lacrimal)	5.3	5.2		4.5		
Min. interorbital width	2.5	2.4		1.9		
Zygomatic width	8.5	8.8		7.5		
Mastoid width	(8.9)			7.5	8.3	
Rostral height	4.3	4.4		4.0	4.6	
Braincase height (max.)	7.9	7.2		6.6	7.3	
Palate length	1.6	1.6		1.7	1.5	
Palatal width (base of M ²)	3.0	3.2		2.7	3.0	
Interperiotic distance	1.4	1.5				
C1-M3			5.6			
P4-M3			5.0	(4.1) (4.1)	4.3	
M1-M3			3.5	(3.3) (3.2)	3.5	
C ¹ L			1.4			
C ¹ W			1.1			
P ⁴ L		0.9	1.1	(0.9) (1.0)	0.9	1.1
P ⁴ W		1.1	1.3	(1.0) (0.9)	1.3	1.2
M ¹ L		1.4	1.5	(1.3) (1.3)	1.3	1.4
M ¹ W		1.4	1.4	(1.1) (1.1)	1.5	1.3
M ² L	(1.3) (1.3)	1.3	1.3	(1.2) (1.3)	1.3	1.3
M ² W	(1.4) (1.4)	1.5	1.4	(1.2) (1.2)	1.5	1.4
M ³ L		1.0	0.9	(0.8) (0.9)	0.9	
M ³ W		1.3	1.4	(1.1) (1.2)	1.5	

Premaxillae not known but make a V-shaped junction (often stepped) with the maxillae rather than a rounded V-shape as in *R. aurantius* and *B. nooraleebus*. Palate shorter, with posterior margin extending to the level of the metacone of M² (rather than the anterior face of M³), marked by a short postpalatal spine, as in *R. aurantius*. Mesopterygoid fossa narrow anteriorly, necking in before broadening posteriorly, more similar to *R. aurantius* than *B. nooraleebus* in which it is broad and rounded anteriorly and of uniform width throughout its length.

Lacrimal foramen much larger than in *R. aurantius* and larger than in *B. nooraleebus*. Lateroventral fossa broader than in *R. aurantius* and similar in width to *B. nooraleebus*. Postpalatal and sphenopalatine foramina much larger than in *R. aurantius* or *B. nooraleebus* (QM F19039 but not 19040), closely paired, more distant in *R. aurantius* and well separated in *B. nooraleebus*.

Anterior diploic, ethmoidal and cranio-orbital foramina fused, larger than in *B. nooraleebus*, not fused and large in *R. aurantius*, separated from the optic foramen by a thick bar (rather than broader plate) of bone. Like *R. aurantius*, palate pierced by many foramina, none especially distinctive.

Sphenorbital bridge relatively broad, not greatly constricted posteriorly, with sphenorbital fissure well-exposed. Hammular process very similar to *R. aurantius*, with a conspicuous wing projecting backwards making up at least half its length, with a laterally directed flange of variable length (long in QMF22859) posterior to the hammular process, as in *R. aurantius* and *B. nooraleebus*. Sphenorbital fissure shorter and broader than in *R. aurantius*; optic foramen more lateral than in *R. aurantius*, with the orbitosphenoid splint separating them directed medially rather than posteromedially as in *R. aurantius* and *B. nooraleebus*.

Basisphenoid shallow. Basisoccipital width between the periotics as in *R. aurantius* (perhaps slightly narrower), narrower than in *B. nooraleebus*. Postglenoid fossa (?temporal emissary foramen) larger than in *R. aurantius* and *B. nooraleebus*; postglenoid process also slightly better developed than in *R. aurantius*, and much better than in *B. nooraleebus*. Foramen ovale very large; a bar of bone separating the foramen ovale from a ?posteriorly opening fenestra in *B. nooraleebus* is absent in *R. tedfordi* and *R. aurantius* as is the fenestra. The lambdoidal crest is better developed than in *B. nooraleebus*, and in this way more similar to *R. aurantius* (although in the latter this varies intraspecifically e.g. AR 15400 and M8416). Unlike *R. aurantius*, it is continuous across the occipitals in *R. tedfordi* rather than attenuating at the ?nuchal point. Foramen magnum more dorsally oriented than in *B. nooraleebus* and *R. aurantius*, with indentation of its dorsal margin in *R. aurantius* lacking in *R. tedfordi* and *B. nooraleebus*.

Periotic, its orientation and its attachment to surrounding basicranial elements similar to that in *R. aurantius* and *B. nooraleebus*.

Upper teeth approximately the same size in the 3 species, those of *R. aurantius* more hypsodont. Upper incisors unknown. C^1 similar to that in *B. nooraleebus* in width, length and posterior secondary cusp, but with shallower anterolingual cingulum, removing its squared appearance (but see QMF22845). C^1 wider and longer in the tooth row than in *R. aurantius*. P^2 extruded such that C^1 and P^4 are in close contact, almost touching (e.g. QMF22845), being closer than in *B. nooraleebus* (although this varies) and at least as close as in *R. aurantius*. P^4 narrower than in *R. aurantius* (especially anteriorly), the lingual cingulum deeper than in *R. aurantius* and similar to *B. nooraleebus*, and the anterolingual cingular cusp better developed than in *R. aurantius*. M^1 with 4 roots, with heel similar to *R. aurantius* and broader than in *B. nooraleebus*, with a very strong dihedral crest and thickened posterolingual cingulum. Lingual notch incipient, well-developed in QMF22840. M^2 with 4 roots, evenly spaced, as in *R. aurantius*; *B. nooraleebus* with 3. Its heel much weaker than in *R. aurantius*, similar to *B. nooraleebus* but with the postprotocrista reaching the base of the metacone and with a slight ridge (rather than crest) issuing from its end point (or more anteriorly in worn specimens) and extending to the slightly thickened posterolingual cingulum. M^3 similar in the 3 taxa.

COMPARISON. This species differs from the Recent *R. aurantius* in its smaller size, relatively shorter braincase (especially in the postglenoid region), flattened rostral inflations, deep groove between inflations, strong supraorbital ridges, C^1 with less pronounced posterior accessory cusp, P^2 relatively narrow with greater anterobuccal extension and M^2 heel much less expanded.

From Riversleigh's *Brachipposideros nooraleebus* Sigé et al., 1982 it differs most conspicuously in its relatively shorter palate with posterior medial spine, its long, slim mesopterygoid fossa, well-developed sagittal and lambdoid crests, more inflated nasals, C^1 without deep anterolingual cingulum, M^1 with broader heel and M^2 with four roots.

It differs from *B. omuni* Sigé, 1995, *B. sp. cf. B. branssatensis* or 'Form X' from St Victor La Coste (Sigé et al., 1982), *B. sp. cf. B. branssatensis* from La Colombière (Sigé et al., 1982) and *B. agulari* Legendre, 1982 in M^2 having 4 roots. It differs from *B. collongensis* (Depéret, 1892) and *B. dechaseauxi* Sigé, 1968 in the heel of M^{1-2} not being posterobuccally extended and M^2 invariably having 4 roots. It differs from *B. branssatensis* (Hugueney, 1965) in its posterolingual development of the heel of M^{1-2} and generally less conspicuous lingual notch separating protocone from heel in M^{1-2} .

Brachipposideros Sigé, 1968

?*Brachipposideros watsoni* sp. nov. (Figs 3-4, Table 1)

ETYMOLOGY. For Neil Watson in recognition of his long association with the University of NSW.

MATERIAL. Holotype QMF22915, skull with LP^2 - M^3 and RP^2 - M^3 . Paratypes QMF22828, skull with LC^1 - M^3 and RP^2 - M^3 , QMF22916, maxillary fragment with LC^1 - M^2 . Other material QMF22824, QMF22826, QMF22833, QMF22846, QMF22857, QMF22860, QMF22861, QMF22862, QMF22870, QMF22894, QMF22896, QMF22898, QMF22900, QMF22904, QMF22907. All material from the early Miocene Bitesantennary Site (discussed above).

DESCRIPTION. ?*Brachipposideros watsoni* is described in comparison with the Miocene *R. tedfordi* sp. nov., *B. nooraleebus* Sigé et al., 1982 and Recent *R. aurantius* (Gray, 1845).

Skull approximately 10% shorter and narrower than *R. tedfordi*, 20-30% shorter than *R. aurantius*, with braincase length similar to *B. nooraleebus*, with similar overall proportions to *B. nooraleebus* and *R. tedfordi*, rather than *R.*

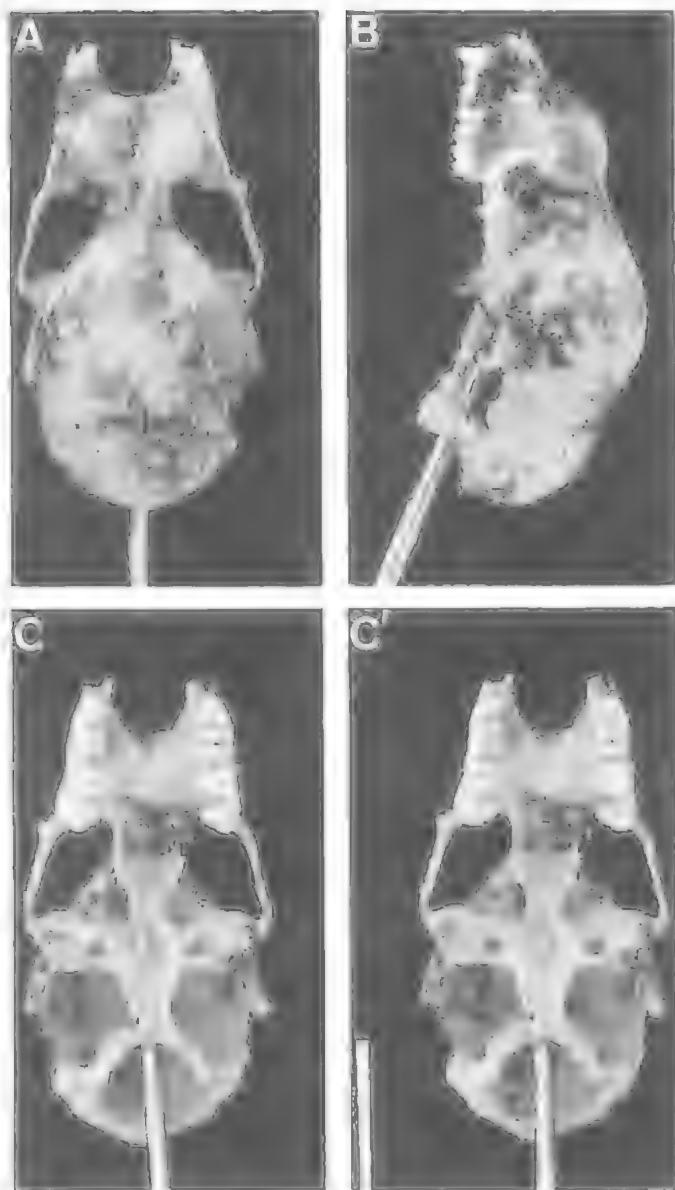


FIG. 3. ?*Brachipposideros watsoni* sp. nov., QMF22915, holotype, from Bitesantennary Site, Riversleigh, northwestern Queensland. A, dorsal view; B, lateral view; C-C', ventral view, stereopairs. Scale indicates 5 mm.

aurantius (latter much longer in the postglenoid region), with lambdoidal crest generally weaker than in *R. tedfordi*, more like *R. aurantius* and *B.*

nooraleebus, with rounded posterior margin. Sagittal crest lower anteriorly than in *R. tedfordi* and *R. aurantius* but probably slightly taller than in *B. nooraleebus*. As in *B. nooraleebus*, maximal height of braincase more posterior than in *R. tedfordi* and *R. aurantius*, being posterior to the glenoid; sagittal crest remaining tall anteriorly onto the postorbital region (unlike *R. aurantius*), joining the supraorbital ridges fairly distinctly (in QMF22828 supraorbital ridges almost develop wings or flattened plates like an incipient frontal shield), of variable posterior extent (in QMF22915 attenuating in the parietal region, as in *B. nooraleebus* and *R. aurantius*, but in QMF22828 and QMF22843 extending to the lambdoidal crest as in *R. tedfordi*). Zygomatic width greater than mastoid width as in *R. tedfordi* and unlike *R. aurantius*.

Rostrum lower than braincase (not as low as in *R. aurantius* and *R. tedfordi*). Rostral inflations similar in proportion to *R. tedfordi* and *R. aurantius*, more distinct than in *B. nooraleebus*, less distinct than in *R. tedfordi* and *R. aurantius*. Trough between the inflations less pronounced than in *R. tedfordi* but more than in *R. aurantius* and slightly more than in *B. nooraleebus*. Frontal depression shallower than in *R. tedfordi* but deeper than in *R. aurantius* and *B. nooraleebus*, with an unpaired medial frontal foramen. Nasal opening dorsoventrally compressed in anterior view compared to that in *R. tedfordi* and *R. aurantius*; bony nasal septum much longer than in *R. tedfordi* and similar to *R. aurantius*; opening of the vomer sinus round as in *R. aurantius* rather than slit-like as in *R. tedfordi*.

Infraorbital foramen dorsal to M^{2-3} as in *R. aurantius*, rather than M^2 as in *R. tedfordi* and *B. nooraleebus*, more elongate than in *R. tedfordi* and *R. aurantius*. Anteorbital bar slim and generally the same width throughout, as in *B. nooraleebus*, sometimes with a flange or wing, often slightly curved as in *R. tedfordi* and *R. aurantius*. Zygomatic arch with very enlarged jugal projection (QMF22857) extending upwards to at least the level of the upper

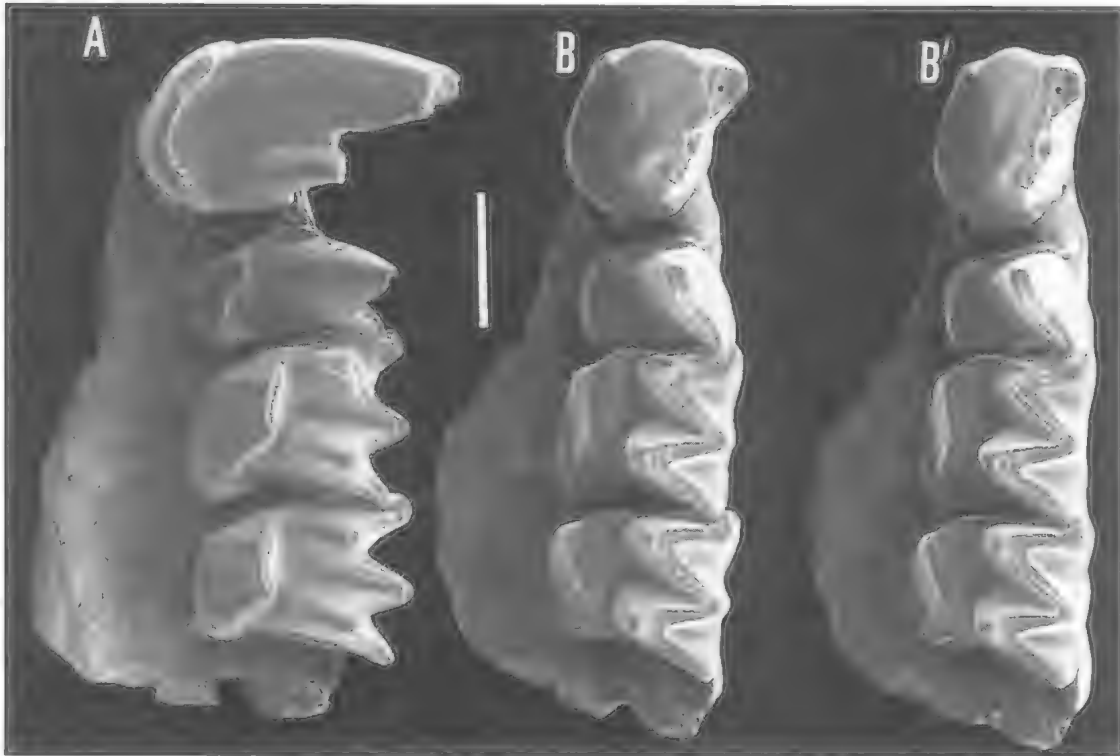


FIG. 4. ?*Brachiposideros watsoni* sp. nov., QMF22916, paratype, maxillary fragment with C¹-M², from Bitesantennary Site, Riversleigh, northwestern Queensland. A, oblique-occlusal view; B-B', occlusal view, stereopairs. Scale indicates 1 mm.

insertion of the anteorbital bar, directed slightly posterodorsally, with a rounded but narrow apex, and slightly convex posterior margin.

Premaxillae unknown, with a V-shaped junction to the maxillae as in *R. aurantius*, *B. nooraleebus* and *R. tedfordi*. Palate extending posteriorly to the level of the anterior face of M¹ as in *B. nooraleebus* and *R. aurantius*, rather than the M² metacone as in *R. tedfordi*. Bony medial palate spine absent, unlike *R. aurantius* and *R. tedfordi* (variable in *B. nooraleebus*). Mesopterygoid fossa more like that in *B. nooraleebus* than in *R. tedfordi* or *R. aurantius*, being broad and rounded anteriorly and uniform in width throughout its length.

Lateroventral fossa narrower than in *R. tedfordi*, broader than in *R. aurantius* and similar in width to that in *B. nooraleebus*. Lacrimal and postpalatal foramina similar to those in *B. nooraleebus* and smaller than in *R. tedfordi*. Lacrimal larger than in *R. aurantius*; postpalatal foramen and sphenopalatine similar in size to *R. aurantius* (but proportionately larger), approximately equidistant from each other and the three

interorbital foramina (cranio-orbital, ethmoidal and frontal diploic), closely paired with the interorbital foramina more distant in *R. tedfordi*, with intermediate condition in *R. aurantius*, with the sphenopalatine not 'confluent' (i.e. 2 small foramina (QMF19038, QMF19039), and the 3 approximately equidistant) in *B. nooraleebus*. Orbitosphenoid splint separating the optic foramen from the sphenorbital fissure, directed posteromedially like in *B. nooraleebus* and *R. aurantius*, rather than medially as in *R. tedfordi*.

Sphenorbital bridge slightly more constricted posteriorly (posterior to pterygoid processes) than in *R. tedfordi* and *R. aurantius*. Pterygoid wings directed dorsally rather than posteriorly, resulting in shorter wings than in *R. tedfordi* and slightly shorter than in *R. aurantius* (proportionately). Postglenoid fossa slightly smaller than in *R. tedfordi*, but slightly bigger than in *R. aurantius*. Postglenoid process similar to *R. aurantius* and *R. tedfordi* and better developed than in *B. nooraleebus*. Foramen ovale similar to the other taxa; a posteriorly directed fossa relatively smaller than in *R. tedfordi* without bar. Inter-

periotic distance similar to that in *R. tedfordi*. Periotic morphology and orientation and attachment to the basicranium similar to other 3 taxa. Foramen magnum similar to that in *R. tedfordi*, directed more ventrally, as in *R. aurantius* and *B. nooraleebus*.

Teeth smaller than in *R. aurantius* and *R. tedfordi*, approximately same size as in *B. nooraleebus*. Upper incisors unknown. C^1 proportionately shorter (in the tooth row) than in *R. tedfordi* and probably *B. nooraleebus*, more similar to *R. aurantius*, C^1 cingulum not developed as in *R. tedfordi* and *B. nooraleebus*, more like in *R. aurantius*: anterolingual cingulum following the tooth outline rather than thickening in the anterolingual corner. Posterior secondary cusp similar to that in *R. tedfordi* but perhaps taller (in buccal view, $1/3$ to $1/2$ C^1 length rather than $1/3$ in *B. nooraleebus* and *R. tedfordi*). P^2 small and buccally extruded; C^1 and P^4 generally not in contact (but see QM F22907), generally closer, but not in contact in *R. tedfordi* and *R. aurantius*. P^4 narrower than in *R. aurantius* and *B. nooraleebus*, most similar to *R. tedfordi*. M^1 has 4 roots, with heel longer than in *B. nooraleebus*, more similar to *R. tedfordi* and *R. aurantius*. M^2 with 3 roots, like *B. nooraleebus* and unlike *R. tedfordi* and *R. aurantius*, with heel more expanded than in *R. tedfordi*, similar to *B. nooraleebus*, much less expanded than in *R. aurantius*. (Buccal and lingual lengths similar in ?*B. watsoni* and *R. tedfordi*; buccal length greater than lingual length in *B. nooraleebus*.) M^{1-2} crest and cingular development and M^3 similar in the 4 taxa.

COMPARISON. It differs from *R. tedfordi* in its slightly smaller size, shorter mesopterygoid fossa, less anteriorly inflated braincase, more elongate infraorbital foramen, lack of postpalatal spine and M^2 with three roots.

It differs from the Recent *R. aurantius* in its smaller size, much less anteriorly inflated braincase and pronounced sagittal crest, relatively shorter braincase (especially in postglenoid region), flattened rostral inflations, deeper groove between inflations, strong supraorbital ridges, less pronounced accessory cusp on C^1 , P^2 larger and less extruded from the toothrow, P^4 relatively narrow with greater anterobuccal extension and M^2 heel much less expanded and having three roots.

It differs from *B. nooraleebus* in its C^1 lingual cingulum being uniformly shallow, its narrower and shorter P^4 , more expanded M^2 heel, sharp rise in braincase height above glenoid, position of

infraorbital foramen, deep frontal depression and more pronounced supraorbital crests.

It differs from *Brachipposideros branssatensis*, *B. collongensis* and *B. dechaseauxi* in M^2 invariably having three roots. It differs from *B. omani* in its larger size and better developed heel in M^2 . It differs from 'Form X' in its more expanded heel in M^2 . It differs from *B. sp. cf. B. branssatensis* in its posterolingual development of the heels of M^{1-2} and pronounced crests on the posterior flank of the protocone. It differs from *B. aguilari* in M^1 having four roots.

COMPARISONS OF THE NEW HIPPOSIDERIDS WITH RELATED TAXA

These new species are similar in skull and dental morphology to northern Australia's living *Rhinonicteris aurantius* and Microsite's *Brachipposideros nooraleebus* in proportions of the skull, broad rostrum, subparallel tooth rows, palate and zygomatic arch, crested premaxillae, basicranial, periotic and otic morphology, pronounced accessory cusp on C^1 and little reduced upper and lower M^3 s.

Sigé et al. (1982) recognised *R. aurantius* as a probable descendant of the Australian *Brachipposideros* lineage. *Brachipposideros* is known from the Tertiary of Europe, Arabia and Australia (Sigé, 1968; Sigé et al., 1982; Legendre, 1982; Ziegler, 1993; Sigé et al., 1995). The new Riversleigh species can be compared with European and North African taxa only on their upper dentition because: 1) skull material has not been described for non-Australian taxa and 2) dentaries cannot be positively referred to the Riversleigh taxa.

A combination of dental characters is shared by *Brachipposideros* and the new Australian taxa: small size, P^2 between C^1 and P^4 near or on buccal margin of tooth row, C^1 with secondary cusp, P^4 slender with respect to other teeth, M^1 with four roots (loss in some), M^2 with three roots (advanced forms have four), heel of M^1 separated from protocone by a notch (loss secondary) and forming a posteriorly directed lobe, M^2 heel relatively weakly developed, primitively, postprotocrista has prominent anterior portion and only incipiently developed posterior part. *Brachipposideros nooraleebus* shares with European *Brachipposideros* a small lower canine, low coronoid process and similar shape of ascending ramus (Sigé et al. 1982).

The 3 Australian Miocene species differ from the early Oligocene *B. omani* (Sigé et al., 1995)

in their larger size, more recurved C^1 with better developed secondary posterior cusp, and M^2 protocone with weaker dihedral crest. Additionally, *R. tedfordi* differs from *B. onani* in its 4-rooted M^2 .

Compared with *B. sp. cf. B. branssatensis* or 'Form X' (Sigé et al. 1982) of the French late Oligocene (Chattian), the Australian species have P^2 smaller and further extruded from the toothrow, P^4 with better developed anterolingual cingular cusp, P^4 wider with respect to M^{1-2} (closest to ?*B. watsoni*), M^{1-2} heels more posterolingually developed and posteriorly directed, M^2 heel more expanded with dihedral crest and posterolingual cingulum stronger in Australian taxa. M^3 size is similar.

The early Miocene (Lower Aquitanian) French species *B. branssatensis* (Hugueney, 1965) has quite different M^{1-2} heel development from Australian species, with heel expansion occurring at the posterolingual corner but directed buccally, and having a pronounced lingual notch, a variable characteristic in Australian taxa. The M^2 heel is better developed than in Australian forms but the dihedral crest is more pronounced in Australian taxa as is (probably) the posterolingual cingulum. C^1 is similar to that in ?*B. watsoni* and *R. tedfordi*, in which the lingual cingulum is uniform and follows the curvature of the tooth, and hence unlike *B. nooraleebus*. P^2 position and size are similar but in Australian forms P^2 is generally smaller and more extruded. The infraorbital foramen occurs dorsal to M^2 as in *R. tedfordi* and *B. nooraleebus*.

M^{1-2} heel expansion in the Australian taxa is more similar to that found in the French early Miocene (Lower Aquitanian) *B. sp. cf. B. branssatensis* from La Colombière, in direction of expansion and strong crest on the posterior flank of the protocone. C^1 is smaller in size and the lingual cingulum uniform and even in depth, but with similar thickening in its anterolingual corner as in *R. tedfordi*. The posterior margin of P^4 is very curved, the anterior margin narrower and the anterobuccal extension greater than in ?*B. watsoni* and similar to *B. nooraleebus*. M^1 , and M^2 ?variably, has 4 roots.

The French early to early middle Miocene (Upper Aquitanian) *B. dechaseauxi* Sigé, 1968 is larger than the Australian species. The posterior flank on the M^{1-2} protocone is simply rounded with the dihedral crest poorly developed, the heel is directed posteriorly to posterobuccally like *B. branssatensis*. M^{1-2} width is very similar to that of M^3 , ?variably developed lingual notch separat-

ing protocone and heel. P^4 is narrow with respect to M^{1-3} , possibly smaller than in ?*B. watsoni*, its anterobuccal extension much greater than in Australian taxa. P^2 is outside the toothrow, but is probably similar to Australian taxa in size and position. C^1 has a uniform lingual cingulum as in ?*B. watsoni* and *R. tedfordi*.

M^{1-2} heel development in the French early to early middle Miocene (Burdigalian) *B. aguilari* Legendre, 1982 is sharper than the Australian species but the direction of expansion and crest on the protocone are similar. The posterolingual heel cingulum is not well-developed. The crest is continuous with the posterior lingual cingulum in *B. aguilari*. In M^{1-2} the ectoloph is different: the buccal edge is angular rather than rounded as in the Australian taxa. P^4 appears to be relatively large and C^1 gracile with a uniformly deep lingual cingulum like ?*B. watsoni*.

The type species, *B. collongensis* (Depéret, 1892), from the French early middle Miocene (Upper Burdigalian) is similar in size to *B. watsoni* and *B. nooraleebus* but P^2 is less extruded from the toothrow, M^{1-2} heels posterobuccally developed like *B. branssatensis* and *B. dechaseauxi* and M^2 heel better developed but with weaker dihedral crest especially in M^2 whose protocone flank is rounded. P^4 is relatively wide with respect to M^{1-3} as in the Australian species.

PHYLOGENETIC RELATIONSHIPS

On dental characters, the new Australian species are more similar to each other and to *B. nooraleebus* than to non-Australian taxa. Sigé et al. (1982, figs 8-9) found that compared to European species, the dental structure of *B. nooraleebus* was more advanced than Aquitanian forms and as advanced as Burdigalian species. The Chattian 'Form X' was considered close to the base of the European radiation, with *B. branssatensis* close to the group that gave rise to the *B. collongensis* and *B. dechaseauxi* lineages and *B. sp. cf. B. branssatensis* closer to *B. aguilari* and *B. nooraleebus*. Apomorphies shared by *B. sp. cf. B. branssatensis*, *B. aguilari* and *B. nooraleebus* included heel of M^{1-2} separated from the protocone by a slight lingual notch and heels developed posterolingually and directed posteriorly. *Brachipposideros aguilari* and *B. nooraleebus* share further reduction of P^2 so that C^1 and P^2 are close and sometimes in contact, P^4 relatively larger and M^{1-2} protocone with pronounced dihedral crest.

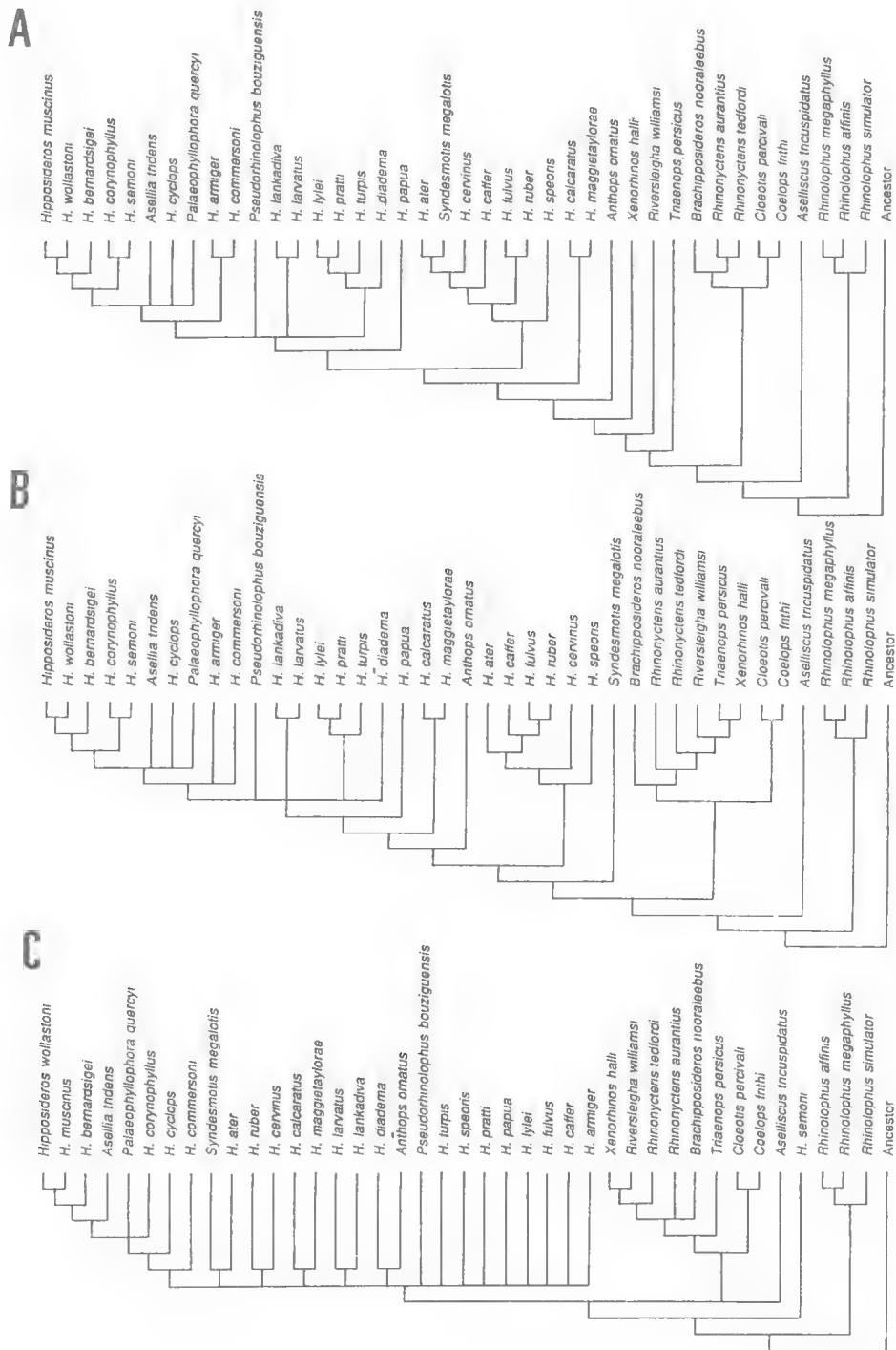


FIG. 5. Phylogenetic hypotheses of hipposiderid relationships presented by Hand & Kirsch (in press) resulting from analyses conducted on 40 taxa and 59 dental, cranial and skeletal characters: A, Strict consensus of 4 PAUP trees, all unordered characters (CI=0.25; 87.5% resolution); B, Strict consensus of 8 PAUP trees, some ordered characters (CI=0.23; 82.5% resolution). C, Hennig86 Nelson consensus, unordered characters. See Hand & Kirsch (in press) for characters and character states.

TABLE 2. Distribution of character-states used in a phylogenetic analysis of relationships among *Brachipposideros* and *Rhinonictis* species, and related taxa, based on dental characters only. 0=interpreted plesiomorphic condition, 1-3=apomorphic states, ?=missing data or character does not apply.

Taxon	Character states
<i>B. omani</i>	?1?? ??? 01 ?11
<i>B. brassatensis</i>	100? 0011 01 011
<i>B. sp. cf. B. branssatensis</i>	1000 0011 01 011
<i>B. collongensis</i>	1011 0101 11 011
<i>B. aguilari</i>	1012 1122 01 011
<i>B. dechaseauxi</i>	1010 0011 11 011
<i>B. nooraleebus</i>	1002 0022 01 011
? <i>B. watsoni</i>	1001 0022 01 011
<i>R. tedfordi</i>	1012 0022 11 011
<i>R. aurantius</i>	1012 0122 12 011
<i>Hipposideros ater</i>	0201 ?022 01 111
<i>Anthops ornatus</i>	0100 ?021 ?0 100
Ancestor	0000 0000 00 000

Characters:

- 1: Height of ascending ramus of dentary: 0=tall, 1=low
- 2: C¹ accessory cusp: 0=present, 1=poorly developed, 1=absent
- 3: P² extrusion: 0=extruded but still separating C¹ and P⁴, 1=C¹ and P⁴ in contact or nearly so
- 4: P⁴ width wrt other cheekteeth: 0=narrow, 1=medium, 2=wide
- 5: M¹ no. of roots: 0=4, 1=3
- 6: M¹ heel development/length: 0=moderate, 1=strong
- 7: M¹ heel direction: 0=none, 1=posterobuccal, 2=posterolingual
- 8: M¹ lingual notch: 0=absent, 1=inconspicuous, 2=conspicuous
- 9: M¹ dihedral crest: 0=absent, 1=weak/medium, 2=strong
- 10: M² number of roots: 0=3, 1=4
- 11: M² heel length/development: 0=none, 1=slight, 2=great
- 12: M² heel direction: 0=none, 1=posterobuccal, 2=posterolingual
- 13: M² dihedral crest: 0=absent, 1=weak/medium, 2=strong

The new Bitesantennary species also share these apparent apomorphies and are assigned to that clade. Although *tedfordi* shares with the *B. branssatensis*, *B. collongensis* and *B. dechaseauxi* lineages a fourth root on M² it does not share the distinctive posterobuccally expanded heels on M¹⁻². In this case a four-rooted M² is interpreted to be homoplastic; it occurs also in *R. aurantius*.

A phylogenetic analysis of the interrelationships of 12 hipposiderid species including 10

species of *Brachipposideros* and an hypothetical ancestor, based only on dental features (13 characters) (Table 2) and using the clustering program PAUP 3.1.1 (Swofford 1993), was unable to resolve relationships within the group (percent resolution of trees 18.2%). Tree resolution did not improve when the most poorly known species, *B. omani*, was removed, nor if character states were ordered. However, majority rule trees (50%) did show the European *B. branssatensis*, *B. dechaseauxi* and *B. sp. cf. B. branssatensis* (Form X) clustering in 67% of trees, as did *B. collongensis*, *B. aguilari*, *R. tedfordi* and *R. aurantius*. Hand & Kirsch (in press) found in their phylogenetic analyses of 37 hipposiderids that dental features (20 characters) were not sufficient to interpret relationships among genera and species groups of the Hipposideridae. They found that resolution of trees was less than 33% when dental features only were used, compared with 87.5% resolution with a combined data set of cranial, dental and skeletal characters.

Brachipposideros Sigé, 1968 was erected as a subgenus of *Hipposideros* Gray, 1831. However, probable patristic relationships between *Brachipposideros* and *Rhinonictis*, indicate that the evolutionary relationships of these taxa are not adequately reflected by current taxonomy. Hand & Kirsch (in press) found *Hipposideros* to be almost certainly paraphyletic, as did Bogdanowicz & Owen (in press). Huguency (1965), Sigé (1968) and Legendre (1982) all suggested that *Hipposideros* was paraphyletic.

Hand & Kirsch (in press) also found that *B. nooraleebus* was more closely related to *Rhinonictis* (*aurantius* and *tedfordi*), and possibly other Australian Miocene hipposiderids than to *Hipposideros* (Fig. 5A-C). Because that analysis was based on cranial as well as dental characters, European *Brachipposideros* taxa could not be included, and precise relationships between non-Australian and Australian *Brachipposideros* species remain unclear.

Relationships between *Brachipposideros*, *Rhinonictis* and other Australian Miocene hipposiderids were not completely resolved in the analyses by Hand & Kirsch (in press). However, in all trees *nooraleebus* occurred as the plesiomorphic sister-species to a clade consisting of, or containing, *aurantius* and *tedfordi*. In some trees, *aurantius* and *tedfordi* formed part of a broader group of Australian Miocene hipposiderids including *Xenorhinos* and *Riversleigh* (Fig. 5B-C).

When *watsoni* was included in PAUP analyses

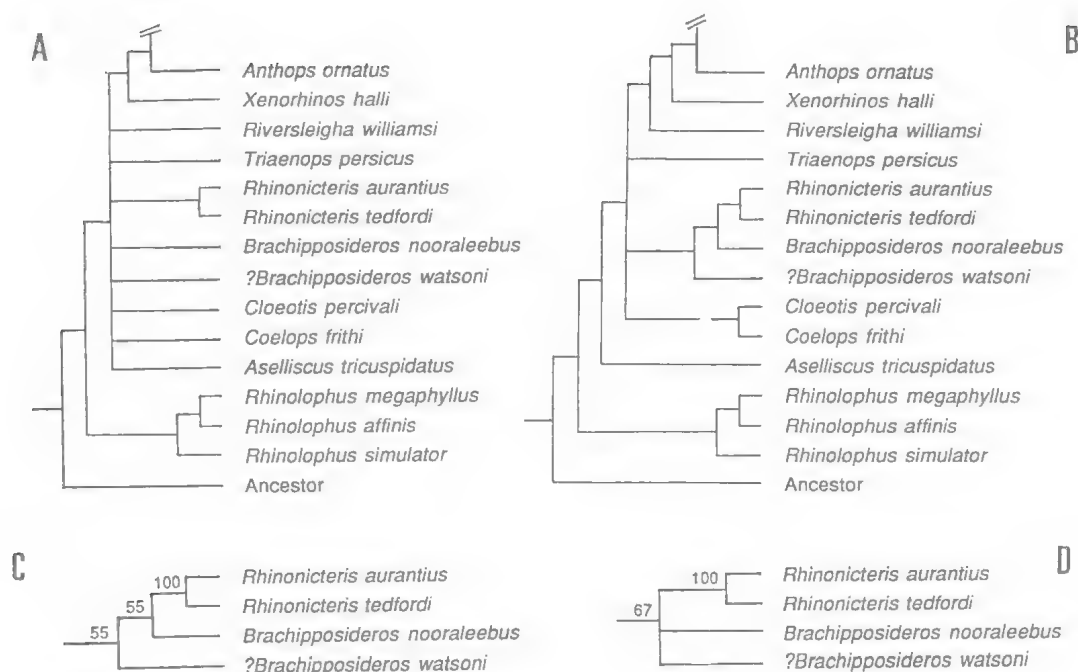


FIG. 6. Phylogenetic hypotheses of relationships of 40 hipposiderids plus *?Brachipposideros watsoni* resulting from PAUP analyses conducted on 59 characters (Hand & Kirsch, in press). A, Strict consensus of 44 trees (CI=0.24; 55% percent resolution), all unordered; B, 50% majority rule tree of 6A; C, D, % support (majority rule) for clustering of *Rhinonictis* and *Brachipposideros* taxa, trees based on unordered and ordered characters respectively.

of the same taxa and characters used by Hand & Kirsch (in press), resolution of relationships between hipposiderid taxa fell (from over 82% to less than 60% in all analyses). Relationships among crown groups (i.e. *Hipposideros*, *Asellia*, *Palaeophyllophora* and *Pseudorhinolophus*) remained unchanged from those shown in Fig. 5 (indicated by broken line in Fig. 6A-B), but resolution at the base of the trees (e.g., among *Brachipposideros*, *Rhinonictis*, *Coelops* and *Cloeotis*) decreased markedly (cf. Figs 5A and 6A). Majority rule trees (50%) clustered species of *Rhinonictis* and *Brachipposideros* (e.g., Fig. 6B), but with little consensus on relationships between *watsoni*, *nooraleebus* and an *aurantius*-*tedfordi* clade (Fig. 6C-D).

On the basis of all analyses (Hand & Kirsch in press and herein), *watsoni* and *tedfordi* are assigned to a clade also containing *B. nooraleebus* and *R. aurantius*. However, the interrelationships

between these taxa is not as clear. Skull morphology of *nooraleebus* (e.g., its poorly developed sagittal crest, shallow frontal depression and poorly inflated nasals) is less derived than that of *watsoni*, but its dentition (e.g., large P^4) would exclude it from being a structural ancestor to *watsoni*. Here, *watsoni* has been tentatively assigned to *Brachipposideros*, and *tedfordi* to *Rhinonictis*. *Brachipposideros nooraleebus* is known from fragmentary material with key features of the sphenorbital bridge area lacking (Hand, 1993, fig.1). However, both *nooraleebus* and *watsoni* lack a number of apparent apomorphies shared by *tedfordi* and *aurantius*, including an anteriorly vaulted braincase and low but conspicuously inflated rostrum, a round infraorbital foramen bordered by a curved anteorbital bar, a postpalatal spine, a narrow, scalloped mesopterygoid fossa, a poorly (posteriorly) constricted sphenorbital bridge with long (an-

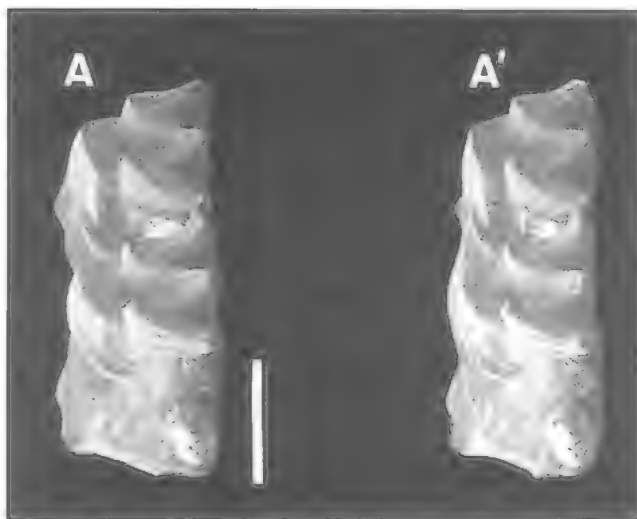


FIG. 7. ?*Brachipposideros* sp., QMF22917, maxillary fragment with M^{1-2} , from Upper Site, Riversleigh, northwestern Queensland. A-A', stereopairs, oblique-occlusal view. Scale indicates 1 mm.

teroposteriorly) pterygoid wings, and M^2 with four (rather than three) roots. Fewer apomorphies appear to be shared between *watsoni* and *nooraleebus*, but potentially include the posterior extension of the supraorbital crest and elongated infraorbital foramen.

Recent *R. aurantius* can be distinguished from the Miocene *R. tedfordi* by its larger size, relatively longer braincase (especially in postglenoid region), little or no groove between inflations, weaker supraorbital ridges, more expanded heel on M^2 , more pronounced accessory cusp on C^1 , P^4 relatively wide with little anterobuccal extension, and P^2 small and further extruded. In Riversleigh's Pliocene Rackham's Roost deposit, an early population of *R. aurantius* occurs syntopically with other as yet undescribed *Rhinonictoris* and/or *Brachipposideros* species, and today *R. aurantius* is still found in the general area.

DISCUSSION

I raise *Brachipposideros* Sigé, 1968 from subgeneric to generic level. Tentatively, it would include non-Australian species *B. branssatensis*, *B. collongensis*, *B. dechaseauxi*, *B. omani*, *B. aguilar* and *B. sp. cf. B. branssatensis* as well the Australian Miocene species, *nooraleebus* and *watsoni*. Although this may be a paraphyletic group, evidence is conflicting and relationships between Australian and non-Australian taxa are

difficult to determine on dental morphology alone. Until further information becomes available, all non-Australian and the least derived Australian taxa (i.e., those lacking obvious synapomorphies for *Rhinonictoris*) are referred to *Brachipposideros* as perhaps the simplest, if not entirely accurate, reflection of the group's evolutionary relationships.

?*Brachipposideros* sp. (Fig. 7), a maxillary fragment of a Miocene hipposiderid from Riversleigh's Upper Site, preserves M^1 and M^2 which are strikingly similar to those of the *B. collongensis* and *B. branssatensis* lineages, particularly in their posterobuccally-directed heel development which is quite unlike any other known Riversleigh hipposiderid.

The Bitesantennary Site is a Miocene cave-fill in which ?*B. watsoni* and *R. tedfordi* occur with at least 8 other hipposiderids, 5 of which are yet to be described. Five of the 10 Bitesantennary hipposiderids, including ?*B. watsoni* and *R. tedfordi*, are well represented, each by tens or hundreds of complete skulls; the other 5 hipposiderids, and a megadermatid (cf. *Macroderma godthelpi*), are represented by fewer, more fragmentary specimens. The generally very fine preservation of the remains (often with periotics in situ) suggests that fossilisation occurred quickly with little transport, probably in still water rather than guano (in which biodegradation would be expected). Few juvenile bats are among the thousands represented, suggesting that this cave (or part thereof) was not used as a maternity roost.

By analogy with modern bat communities, the high diversity of hipposiderids in the Bitesantennary deposit suggests warm, humid conditions in the cave, and probably outside it. In Europe, appearance of *Brachipposideros* in the fossil record coincides with a period of steadily increasing temperature and their disappearance probably correlates with the climatic deterioration across Europe in the later Pliocene (Aguilar et al., in press). In Australia, 6 hipposiderids are restricted to northern tropical areas. *Rhinonictoris aurantius* roosts in very warm, humid caves in colonies of 20 to several thousand individuals from NW Queensland to NW WA. It emerges at dusk to feed, mostly on moths but also on beetles, shield-bugs, parasitic wasps, ants, chafers and weevils (Jolly & Hand, 1995). Although *R. aurantius* and the Miocene *Rhinonictoris tedfordi*

are closely related and similar in many skull features, the extinct species lacks the forward-projecting development of the sagittal crest that characterises *R. aurantius*, and it is unclear whether or not they could be described as ecological vicars.

Hipposiderid bats promise to be useful biostratigraphic indicators in the limestones at Riversleigh. They are the most common bats in Riversleigh's Miocene deposits, the best preserved, and, with megadermatids, currently the best understood in terms of their phylogenetic relationships as well as their morphological variability (Sigé et al., 1982; Hand, 1993, 1995, 1997). *Brachipposideros nooraleebus* is known only from Microsite and ?*B. watsoni* only from Bitesantennary Site. *Rhinonictis tedfordi*, however, is known from Bitesantennary Site in the Verdon Creek Sequence, RV and Upper Sites on Godthelp's Hill, and White Hunter Site on Hal's Hill. None of the species described herein has been recorded from System C sites (Archer et al., 1989, 1994; Creaser, this volume), but close relatives (?descendants) occur at sites such as Gotham City and Dome North Sites suggesting that lineages may be identified within the Riversleigh limestone sequence.

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MIOPHYLLORHINA RIVERSLEIGHENSIS GEN. ET SP. NOV., A MIOCENE LEAF-
NOSED BAT (MICROCHIROPTERA: HIPPOSIDERIDAE) FROM RIVERSLEIGH,
QUEENSLAND

SUZANNE HAND

Hand, S.J. 1997 06 30: *Miophyllorhina riversleighensis* gen. et sp. nov., a Miocene leaf-nosed bat (Microchiroptera: Hipposideridae) from Riversleigh, Queensland. *Memoirs of the Queensland Museum* 41(2): 351-354. Brisbane. ISSN 0079-8835.

A new Australian Tertiary hipposiderid is described on the basis of a maxillary fragment from RV Site, on Godthelp Hill, Riversleigh, northwestern Queensland. *Miophyllorhina riversleighensis* gen. et sp. nov. is distinguished from all other hipposiderids in its loss of P², retention of a large M³, and P⁴ longer than wide with well-developed anterolingual cingular cusp. Its phylogenetic relationships to other hipposiderids are obscure. — *Miocene Riversleigh, Australia, hipposiderid, leaf-nosed bat*

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Tertiary deposits in the Riversleigh World Heritage Fossil Site, Lawn Hill National Park, NW Queensland are rich in Old World bats of the Hipposideridae (Sigé et al., 1982; Hand, 1993, 1995, 1997). They comprise the majority of bats in all Riversleigh Oligocene-Miocene sites, with as many as 8 species occurring syntopically in deposits such as Upper Site (Archer et al., 1994). Many species are known from complete or nearly complete skulls as well as disarticulated but complete postcranial material. Several hipposiderid genera or subgenera are represented and others await description.

A fragment of a maxilla from RV Site (Archer et al., 1989, 1994; Creaser, 1997) represents a new hipposiderid genus distinguished by a unique combination of features. It has not been identified from adjacent, possibly contemporaneous deposits, such as the better-sampled RSO Site (Creaser, 1997). Other vertebrates from RV Site are generally fragmentary and of small to medium-sized animals. They include a skink, madtsoiid, small crocodile, chelid, peramelid, pseudocheirid and the phascolarctid *Nimiokoala greystanesi* (Black & Archer, 1997). Other bats from the site include *Rhinonicteris tedfordi* (Hand, 1997) which also occurs at adjacent sites, a vespertilionid possibly *Leuconoe* and a molossid.

Dental terminology follows Sigé et al. (1982). Specimens held in the fossil collections of the Queensland Museum (QMF), Brisbane.

SYSTEMATICS

Suborder MICROCHIROPTERA Dobson, 1875

Superfamily RHINOLOPHOIDEA Weber,
1928

Family HIPPOSIDERIDAE Miller, 1907

***Miophyllorhina* gen. nov.**

TYPE SPECIES. *Miophyllorhina riversleighensis* sp. nov.

ETYMOLOGY. Greek *phyllo*, leaf and *rhina*, nose; *Mio*- refers to the interpreted Miocene age.

DIAGNOSIS. P² lost; P⁴ longer than wide, with deep lingual cingulum and well-developed anterolingual cingular cusp; large M³, as wide as M² and with premetacrista 3/4 paracrista length.

***Miophyllorhina riversleighensis* sp. nov.**
(Fig. 1)

MATERIAL. Holotype QMF30566, a left maxilla fragment with P⁴, M²⁻³ from Early Miocene tuff at RV Site in System B on Godthelp's Hill, Riversleigh (Archer et al., 1989, 1994; Megirian, 1992; Creaser, 1997). RV Site is perhaps slightly younger than the South Australian Kutjamarpu Local Fauna (Woodburne et al., 1985).

ETYMOLOGY. For the Riversleigh World Heritage Fossil Site.

DIAGNOSIS. As for genus.

DESCRIPTION. Teeth worn but not broken. Alveolus for C¹ indicating this tooth wider and longer than P⁴. P² lost, with no sign of an alveolus for this tooth either within or extruded (lingually or buccally) from the toothrow. P⁴ longer than



FIG. 1. *Miophyllorhina riversleighensis* gen. et sp. nov. from RV Site, Godthelp's Hill, QMF30566, holotype. A, antero-occlusal view showing lack of alveolus for P^2 . B-B', stereopair, oblique occlusal view. Scale = 1 mm.

wide, narrower particularly anteriorly than M^3 and as long. Lingual cingulum deep, well-developed; anterolingual cingular cusp well-developed. M^1 and M^2 with 4 evenly-spaced roots. M^2 with a posteriorly-directed, small but conspicuous heel. Protofossa probably open posteriorly but with wear the postprotocrista reaching the base of the metacone. Postprotocrista with a slight ridge or crest issuing from what was probably its end point (more anteriorly in this worn specimen) and extending to the thickened posterolingual cingulum. M^3 not greatly reduced, as wide as M^2 , with premetacrista $3/4$ paracrista length.

MEASUREMENTS(mm). Holotype QMF 30566:- P^4 - M^3 L=3.77; C^1 (alveolus)- M^3 =4.71; M^2 - M^3 =1.77; P^4 L=0.88; P^4 I=0.81; M^2 L=1.18; M^2 I=1.42; M^3 L=0.82; M^3 I=1.40.

COMPARISONS. In lacking a P^2 , this species differs from all other Riversleigh hipposiderids, namely, *Brachhipposideros*, *Rhinonictis*, *Xenorhinos*, *Riversleigha* and *Hipposideros bernardsigei* from the Oligocene-Miocene Neville's Garden Site (Hand, 1995) and *H. sp.* from the Pliocene Rackham's Roost Site (*H. bicolor* group). The lack of P^2 characterises living and extinct *Asellia*, *Cloeotis* and *H. (Syn-*

desmotis), and P^2 is very reduced or lacking in some members of the *H. cyclops* group (including the only fossil taxon *H. bernardsigei*). It is rarely absent in other extant species of *Hipposideros* (i.e., possibly *H. sabanus*). However, in these cases: 1) M^3 is also very reduced (i.e., *Asellia* and *Hipposideros*); or 2) P^4 is large and anteriorly very wide, with the anterolingual cingular cusp reduced, absent or located near the buccal margin of the tooth (i.e., *Cloeotis percivali* and some of the *H. cyclops* group, including *H. semoni* and *H. stenotis*); or 3) M^3 is reduced and P^4 is wider than long (i.e., *Syndesmotis megalotis*). P^2 is retained in all other hipposiderids, i.e., Tertiary *Palaeophyllophora*, *Pseudorhinolophus* and *Vaylatsia*, and extant *Coelops*, *Paracoelops*, *Triaenops*, *Anthops* and *Aselliscus*. It is also retained in the Rhinolophidae, the immediate sister-group of the Hipposideridae.

DISCUSSION. On available material it is not possible to determine the relationships of this species to other members of this family. Hand & Kirsch (in press) found that dental features alone are not sufficient to interpret relationships within the Hipposideridae.

In its dentition *M. riversleighensis* exhibits a mixture of what appear to be plesiomorphic and apomorphic features. For example, the loss of P^2

is probably a derived feature for hipposiderids, independently acquired in a number of separate lineages. The anteriorly-narrow P^1 with prominent anterolingual cingular cusp is more difficult to interpret, but is possibly plesiomorphic among hipposiderids (Hand, 1995; Hand & Kirsch, in press). The large M^3 on the other hand is probably plesiomorphic among hipposiderids (e.g., *Hipposideros*, *Cloeotis percivali* and the *Brachhipposideros-Rhinonictis* group) but may be secondarily derived in other groups (e.g., the *H. cyclops* group; Hand, 1995).

All hipposiderids known in Riversleigh's Oligo-Miocene and Pliocene sediments retain a P^2 , as do most living Australian hipposiderids (*R. aurantius*, *H. ater*, *H. cervinus*, *H. semoni* and *H. diadema*). Only living *H. stenotis* of NW Australia, a highly specialised member of the *H. cyclops* group (Hand, 1995), lacks a P^2 . *M. riversleighensis* may be related to the *Brachhipposideros-Rhinonictis* group, sharing a similar P^4 and large M^3 .

M. riversleighensis, in lacking a P^2 , may represent an aberrant *Brachhipposideros*. However, no other species of the *Brachhipposideros-Rhinonictis* group shows this abnormality despite hundreds of specimens being available. The other very distinctive bat taxa in RV Site (a vespertilionid and a molossid) lend weight to the argument that *Miophyllorhina* is also a distinctive but poorly represented taxon.

Hand & Kirsch (in press) suggested a close relationship between *Brachhipposideros* and *Cloeotis*, early autapomorphically specialised branches of the hipposiderid radiation. Hill (1982) grouped *Rhinonictis*, *Cloeotis* and *Triacops*; Koopman (1994) referred them to a separate subtribe, the *Rhinonycterina*. Perhaps *Miophyllorhina* is part of this larger group of relatively plesiomorphic hipposiderids. *Cloeotis* shares with *Miophyllorhina* a very large M^3 and lack of P^2 but its P^4 is autapomorphically quite distinct and its M^2 heel very poorly developed.

Alternatively, *M. riversleighensis* could be a distant relative of *H. bernardsigei* of the *H. cyclops* group, interpreted by Hill (1963), Flannery & Colgan (1993) and Hand & Kirsch (in press) as derived hipposiderids. However, although it shares with *Miophyllorhina* a similar M^3 , it retains a reduced P^2 and its P^4 is derived.

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THE FIRST FOSSIL PYGOPOD (SQUAMATA, GEKKOTA), AND A REVIEW OF MANDIBULAR VARIATION IN LIVING SPECIES

MARK N. HUTCHINSON

Hutchinson, M.N. 1997 06 30: The first fossil pygopod (Squamata, Gekkota), and a review of mandibular variation in living species. *Memoirs of the Queensland Museum* 41(2): 355-366. Brisbane. ISSN 0079-8835.

The snake-like Australian pygopod lizards (Pygopodidae in traditional taxonomies) show considerable variation in mandibular and dental structure, correlated with dietary specialisation in several genera. Following a review of this variation, a fully toothed Miocene dentary from Riversleigh, northwestern Queensland, is identified as a pygopod, the first in the fossil record. *Pygopus hortulanus* sp. nov. is specifically distinguishable from living *Pygopus* by tooth morphology and proportions of the symphyseal region of the dentary. ... *Pygopus*, lizards, osteology, fossils, Miocene.

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One of the most distinctively Australian squamate radiations is a group of snake-like, virtually limbless lizards, variously known as flap-footed lizards or snake-lizards (Bustard, 1970). These have no external trace of forelimbs while hind limbs are reduced to fin-like flaps on each side of the vent (Kluge, 1974; Shea, 1993). There are 35 species in 8 genera (Greer, 1989; Shea, 1991; Cogger, 1992). All are restricted to Australia and New Guinea.

Flap-footed lizards have long been regarded as forming a distinct family, the Pygopodidae, closely related to the Gekkonidae (Underwood, 1954, 1957). It has been suggested that the sister group of Pygopodidae is not all Gekkonidae, but only the Australian Diplodactylinae, or some part of that subfamily (Kluge, 1987; King & Mengden, 1990). Acceptance of this phylogenetic hypothesis (dissenting views exist; see Estes et al., 1988) would mean changes in taxonomy, with the diplodactylines becoming a subfamily of the Pygopodidae, as proposed by Kluge (1987) or the pygopodids becoming a subfamily of the Gekkonidae (Bauer, 1990). Pending a consensus view I use Underwood's (1957) contraction of their traditional family name, 'pygopods', as an informal collective term.

Pygopods show considerable ecological and morphological diversity. *Aprasia*, *Pletholax* and *Ophidiocephalus*, exhibit fossorial adaptations and behaviour (Kluge, 1974; Ehmann, 1981; Shea & Peterson, 1993). However, *Pletholax gracilis* and at least some species of *Aprasia* are regularly active on the surface by day (Shea & Peterson, 1993; pers. obs.). Species in the largest genus, *Delma*, and that regarded by Kluge (1974;

1976) as most generally primitive, *Pygopus*, as well as *Lialis*, *Aclys* and *Paradelma*, are surface-dwellers (Wilson & Knowles, 1988; Greer 1989). While most pygopodids appear to be active foragers feeding on invertebrates, the two species of *Lialis* are ambush predators of scincid lizards (Patchell & Shine, 1986a, b; Murray et al., 1991).

The mandibular and dental anatomy of pygopods is varied, and at least partly correlated with the ecological diversity just mentioned. The one overview of pygopod osteology attempted (Stephenson, 1962) gave scant attention to the mandible. Kluge (1974, 1976) employed some mandibular characters in his analysis of the clade, and Rieppel (1984) noted some correlations between anatomy and miniaturisation in *Aprasia* and *Pletholax* when compared to *Pygopus*. Parker (1956) noted sexual dimorphism in *Aprasia*, in which only males have premaxillary teeth.

Australia's fossil lizard fauna is poorly known (Estes, 1983a, b; Covacevich et al., 1990; Hutchinson, 1992); no fossil pygopods have been identified. Fossils are essential for establishing a minimum estimate of the time a taxon has inhabited an area and of the time since the taxon first evolved. If pygopods are the sister group of diplodactylines, especially the Diplodactylini (Kluge, 1987), then it is likely that their differentiation occurred in Australia and should be recorded in the Australian fossil record. This paper is the first report of a fossilised pygopod.

MATERIALS AND METHODS

Dried skeletons (21 species in 8 known genera-Appendix) were examined to assess interspecific

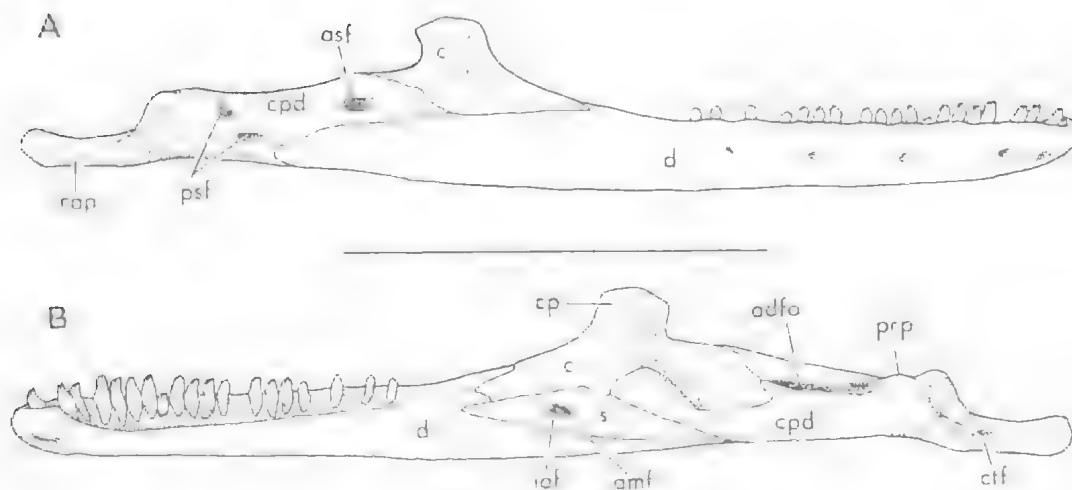


FIG. 1. Labial (A) and lingual (B) views of the right mandibular ramus of a pygopodid lizard, *Delma fraseri* (SAMAR22911, Coomalbidgee, W.A.) showing major features. Abbreviations: adfo=adductor (=Meckelian) fossa; amf=anterior mylohyoid foramen; asf=anterior surangular foramen; c=coronoid; cp=dorsal process of coronoid; cpd=compound bone - fused prearticular, surangular and articular; ctf=foramen for chorda tympani; d=dentary; iaf=inferior alveolar foramen; prp='prearticular process' (medial articular process of the surangular); psf=posterior surangular foramina; rap=retroarticular process; s=splenial. Scale=5mm.

variation in the sutural relationships of the mandibular bones, positions of foramina, tooth number and tooth morphology. With the exception of *Pygopus*, this sample did not permit study of intraspecific variation. Unless otherwise specified, the descriptions refer to the anatomy as seen in intact mandibles. Outgroups used to infer derived character states are diplodactylines as the sister group of pygopods, gekkonines the sister of these two and other scleroglossans as the most distant outgroup (Estes et al., 1988).

PYGPOD MANDIBLE (Fig. 1).

The dentary is the largest bone of the pygopod mandible. It consists of the tooth-bearing body of the bone and a relatively long, posteriorly directed angular process that covers much of the labial and ventral surface of the mandible. Pygopods share with other gekkonoids and members of several other families the complete obliteration by dentary overgrowth of the groove for Meckel's cartilage, but differ, at least from all diplodactylines examined, in that the angular process extends on the labial surface of the mandible to well behind the coronoid (the dentary also extends posteriorly to a marked degree in the gekkonine *Puroedura*, Kluge, pers. comm.). The dentary of diplodactyline and gekkonine geckos

is generally more slender and incurved than that of pygopods and the angular process terminates at about the level of the coronoid. 3-8 mental foramina open along the labial surface of the dentary, the series generally extending posteriorly to 1/2-3/4 the length of the tooth row. There is no posterior extension of the bony internal septum separating the Meckelian cartilage from the inferior alveolar nerve; bony separation is limited to the immediate vicinity of the mental foramina. Estes et al. (1988) described this character (their number 56) in terms which emphasised that a vertically-oriented, posteriorly extended intramandibular septum is well-developed in anguimorphs, but failed to note that it occurs to almost the same extent in lygosomine skinks (Shea & Hutchinson, 1992, fig. 3).

Adult geckos typically have large numbers of small dentary teeth (Bauer & Russell, 1990; Kluge & Nussbaum, 1995); in a sample of 9 diplodactyline, 1 sphaerodactyline and 14 gekkonine genera, dentary counts ranged from 25 (*Phelsuma madagascariensis*) to 62 (*Saltuarius salebrosus*), with a mean of 40.2 (Edmund, 1969; pers. obs.). In adult *Delma* and *Aclys* tooth number is very much like that of diplodactyline and gekkonine geckos, typically in the range 25-35. Reductions to 24 or fewer, or increases to 50 or more are therefore likely to be apomorphic

(Kluge, 1976). Diplodactylines and gekkonines usually have slender, upright teeth with acute crowns bearing a pair of pointed apical cusps separated by a groove (Sumida & Murphy, 1987). Teeth with this morphology occur in some pygopods (*Delma* and *Aclyis*), and are probably plesiomorphic for the group. Within pygopods there is marked intergeneric variation, including robust, upright or slightly recurved teeth, less robust but more strongly recurved teeth, or very small teeth with compressed, sharp-edged crowns. All retain an apical groove, but the bicuspid structure is largely lost, the labial cusp enlarging to become the tooth apex, while the lingual cusp all but disappears. In *Lialis* tooth crowns are so compressed that the apical groove is faint and only discernible in unworn teeth.

The coronoid consists of a laterally compressed dorsal process, an anteriorly-directed dentary process and a posterior process. The dentary process is bifurcated and clasps the dentary bone behind the end of the tooth row both labially and lingually. On the lingual face of the mandible, the anterior extremity of the dentary process terminates posterior to, coextensively with, or anterior to the front of the splenial, the latter 2 character states being apomorphic with respect to other gekkonoids and other lizards. The posterior process of the coronoid extends to the anterior extremity of the Meckelian fossa. The form of the dorsal process varies from tall and fin-like in several genera to very low in *Lialis* (Kluge, 1976). A well-developed dorsal process is the rule in geckoes and other lizards and is likely to be plesiomorphic for pygopods.

The splenial is reduced in all pygopods compared to the development seen in diplodactylines and other geckoes, usually failing to extend anteriorly beyond the level of the distal two or three teeth. In most pygopods the splenial is further reduced in length or depth. The splenial is completely absent in *Aprasia* (pers. obs.; Parker, 1956; 'very slight', Stephenson, 1962). The splenial, when present, completely surrounds (as in diplodactylines) the inferior alveolar foramen and bears a notch for the anterior mylohyoid foramen on its ventral suture with the dentary.

Like the majority of geckoes (Kluge, 1987), pygopods lack a distinct angular. The splenial in *Delma* and *Pygopus* has a posteriorly extending process that separates the dentary and prearticular, as would an angular, suggesting that the angular has been lost via fusion with the splenial.

The surangular is fused labially and posteriorly with the fused prearticular-articular. In adult

pygopods, but is completely distinct in juveniles (*Delma malleri*, *Lialis burtonis* and *Pygopus lepidopodus*). In adults of most genera a suture persists on the lingual face of the mandible running anteriorly from the Meckelian fossa; in intact mandibles this suture may be concealed by the coronoid. 3 foramina are usually present on the labial surface of the surangular. The anteriorly directed opening of the anterior surangular foramen lies on the labial surface on or just posterior to the point of intersection of the sutures between the coronoid, dentary and surangular. 2 other foramina usually lie towards the posterolabial region of the surangular, but there is intergeneric variation. In some pygopods there may be only a single foramen, as in diplodactylines, but in most there are 2. The 2 openings may be close together, or moderately separated, and the more posterodorsal of the 2 may itself be subdivided.

Most lizards have only a single posterior surangular foramen, and so the additional (more anterior) foramen must be identified. Kluge (1967) and Grismer (1988) designated the more ventral of the posterior foramina as the posterior mylohyoid and the more dorsal as the posterior surangular foramen. My survey of gekkonoid mandibular variation suggests that this interpretation is incorrect.

The posterior mylohyoid nerve innervates the throat musculature (Camp, 1923; Poglayen-Neuwall 1954) and typically exits through a medially or ventromedially directed foramen in the angular bone. While the angular is absent in most gekkonoids (Kluge, 1987) some of those examined (the gekkonines *Gekko*, *Phelsuma* and *Phyllodactylus* [= *Christinus*]) retain a small foramen on the dentary-splenial suture in the expected topographic position of the posterior mylohyoid foramen. Other gekkonines and other gekkonoids examined, including all pygopods, lack a foramen in this position.

The foramen identified by Kluge (1967) and Grismer (1988) as the posterior mylohyoid opens on the labial surface of the mandible and runs through to open lingually into the Meckelian fossa. This foramen thus follows the course of the posterior surangular foramen of other lizards, and it too transmits a branch of the mandibular nerve to the adductor (pterygoideus) musculature (pers. obs.). The foramen and nerve are remote from the throat musculature which, by definition, the posterior mylohyoid supplies. It therefore seems to me more probable that the additional foramen on the labial surface of the surangular in pygopods and other gekkonoids represents a duplication of

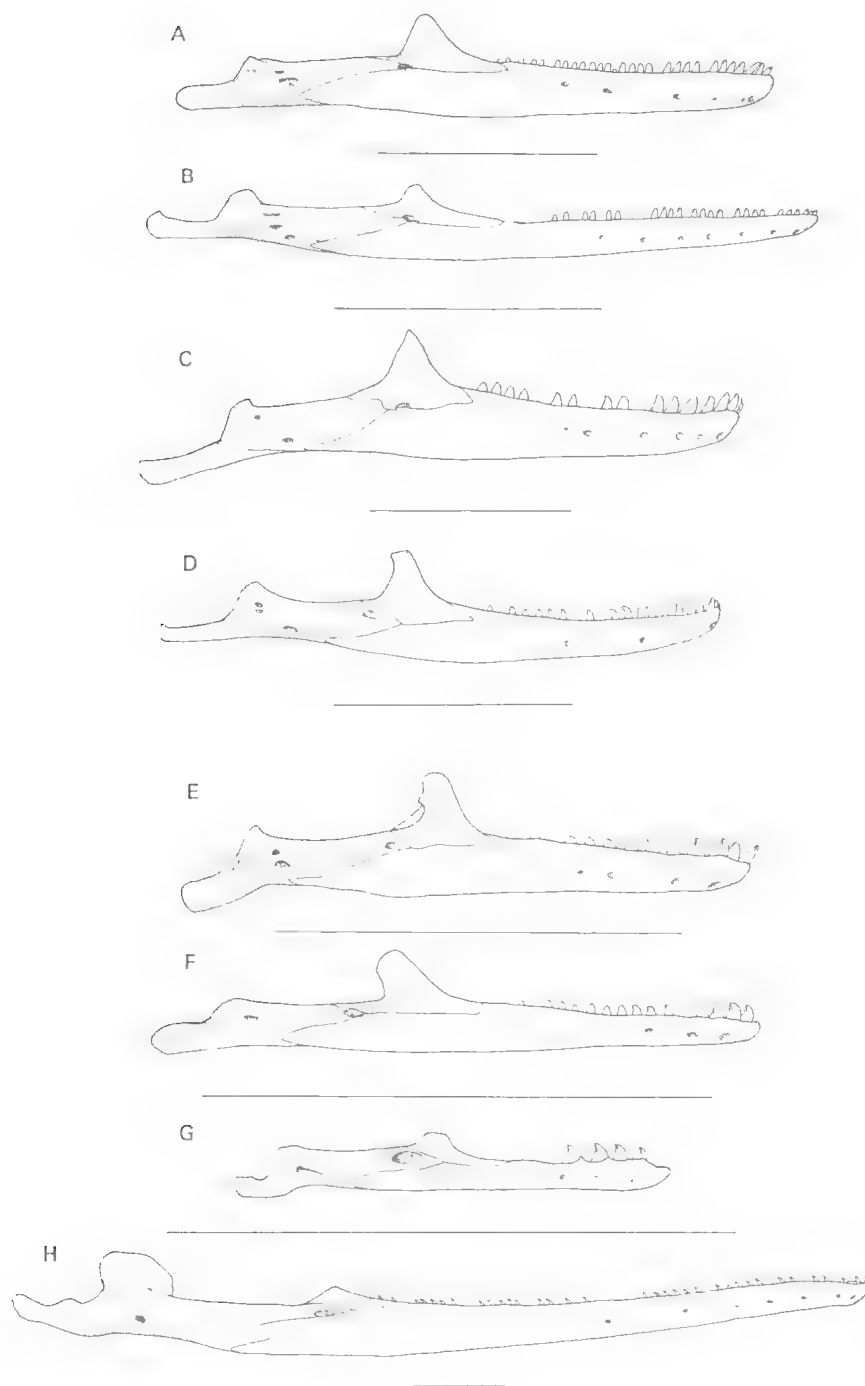


FIG. 2. Labial views of right mandibular ramus of the 8 pygopodid genera. A, *Delma inornata* (SAMAR22408, no data); B, *Aclys concinna* (SAMAR38060, Badgingarra National Park, W.A.); C, *Pygopus nigriceps* (SAMAR21029, no data); D, *Paradelma orientalis* (QMJ30250, Cracow, Qld); E, *Ophidiocephalus taeniatus* (SAMAR28365, Abminga, S.A.); F, *Pletholax gracilis* (SAMAR38061, Jandakot, W.A.); G, *Aprasia striolata* (SAMAR35569, Mylor, S.A.); H, *Lialis burtonis* (NMVD15399, Warby Ranges, Vic.). Scales=5mm.

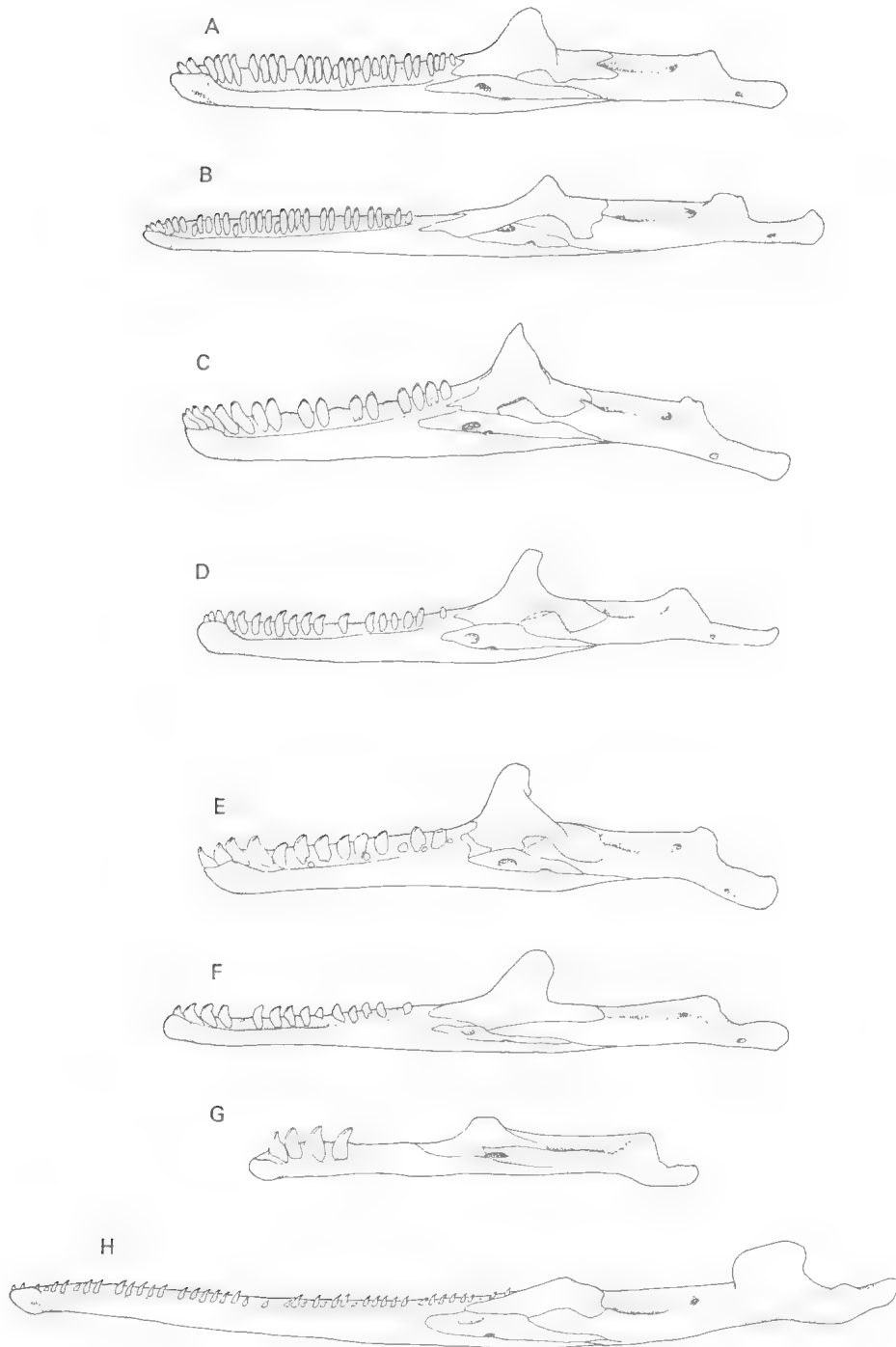


FIG. 3. Lingual views of same specimens in Fig. 2, drawn to same scales.

the posterior surangular foramen, not a displaced posterior mylohyoid.

The fused prearticular-articular together with the surangular constitutes the posterior 1/3 of the pygopod mandible. As in diplodactylines and other gekkonoids the articulating facet is oriented to face posterodorsally rather than dorsally, resulting in a marked 'step' down from the level of the upper edge of the adductor fossa to the level of the retroarticular process. The latter structure is variable intergenerically in its shape (spoon-shaped to rod-like) and the degree of medial or ventral inflection (Kluge, 1976). A foramen for the n. chorda tympani opens on the dorsolingual aspect of the base of the retroarticular process. The posterior region of the Meckelian fossa, which contains the internal opening for the posterior surangular foramen, may be demarcated from the anterior region.

MANDIBULAR VARIATION IN LIVING PYGOPODS

DELMA. This genus has the most generally 'gecko-like' mandibles. However, there is significant variation within the genus in proportions, tooth crown shape, size of splenial and other features. *Delma fraseri* (Fig. 1) and *D. inornata* (Figs 2A, 3A) show some of this variation, with the latter species tending to retain more plesiomorphic features than the former. The pygopod synapomorphy of extensive posterior extent of the dentary on the labial surface is present in all *Delma*, but the teeth are numerous, with unmodified (e.g. *D. impar*, *D. inornata*, *D. nasuta*) or slightly expanded crowns (e.g. *D. fraseri*, *D. mitchelli*). Whether this is inter- or intraspecific variation will require a more extensive survey. Tooth crowns retain the bicuspid morphology of diplodactyline geckoes. The dentary is moderately slender and the splenial little reduced, although it usually fails to extend anteriorly as far as the posteriormost tooth (*D. inornata* specimens showed intraspecific variation, the splenial failing to reach the tooth row in NMVD15448, reaching the second-last tooth in SAMAR35570 and extending as far as the sixth-last in SAMAR22408, Fig. 2A). The posterior surangular foramina are moderately to narrowly separated (variable both inter- and intraspecifically). The relatively unspecialised dentition is associated with a generalised arthropod diet (Shine & Patchell, 1986a; Coulson, 1990).

ACLYS (Figs 2B, 3B). In general the mandible of

this genus is an elongate version of *Delma*'s. Elongation of the jaw occurred by lengthening of the region between the tip of the coronoid process of the dentary and the posterior end of the tooth row, with hypertrophy of the lingual ramus of the anterior process of the coronoid reducing the exposure of the splenial and widely separating it from the tooth row. Height of the dorsal process of the coronoid is reduced relative to most *Delma* and the medial articular process (Fig. 1) of the surangular is elevated, both trends foreshadowing the extensive coronoid flattening and surangular elevation of *Lialis*. The derived features of the jaw of *Aclis* are all seen, although not to the same degree, in some *Delma*, especially those with more elongate skulls such as *D. butleri* and *D. nasuta*.

PYGOPUS (Figs 2C, 3C, 4B, 4D). The mandibles of the two species placed in this genus are very similar to one another, and probably indistinguishable. The form of the mandible is apomorphic with respect to that of *Delma* in being shorter and deeper. The dentition is also apomorphic, the teeth being fewer (<25), much more robust, and with sharp, tapering, recurved crowns. The tooth crowns retain a pronounced apical groove, but the typical gekkonoid bicuspid structure is reduced, with the labial cusp being the principle tooth apex while the lower, lingual cusp is little more than the acute-angled inner margin of the apical groove. The mandible is more plesiomorphic than most *Delma* in that the splenial extends forward to underly the posteriormost teeth. The posterior surangular foramina are moderately to widely separated (intraspecifically variable). The genus is characterised by a pronounced mesio-distal decrease in tooth size, the mesial teeth (second to fifth) being 30-40% taller than the mid-dentary teeth (tenth to twelfth). The enlarged teeth at the front of the jaw are somewhat procumbent and are supported by a deep symphyseal region. Pianka (1986) described *P. nigriceps* as a scorpion specialist, and Patchell & Shine (1986a) found that the major prey of *P. lepidopodus* were mygalomorph and lycosid spiders. Possibly the relatively powerful front teeth are adaptations for rapidly disabling such potentially dangerous prey.

PARADELMA (Figs 2D, 3D). This monotypic genus, like *Pygopus*, has a reduced tooth number (21) compared with *Delma* but the teeth are distinctive, being more slender than in *Pygopus* and having recurved crowns. The tooth apices are like

those of *Pygopus* in that the apical groove is present but the lingual cusp is barely developed. Compared with *Pygopus*, the jaw is less robust and more bowed. The diet is unknown.

OPHIDIOCEPHALUS (Figs 2E, 3E). The jaw of this small fossorial form is relatively robust, short and deep, similar in proportions to that of *Pygopus*, but is apomorphic in several characters. The splenial is greatly shortened and shifted posteriorly compared with *Pygopus*. The single jaw examined is distinctive in that the lingual ramus of the anterior process of the coronoid is reduced, exposing the bone beneath. Based on the position of the prearticular-surangular suture exposed below the dorsal process of the coronoid, this anteriorly exposed bone is the surangular. The posterior surangular foramina are narrowly separated. The teeth are similar in to those of *Pygopus*, but are fewer in number (13-15 in adults versus 17-24 in hatchling to adult *Pygopus*) and have moderately recurved crowns. Recorded prey indicates a relatively generalised arthropod diet (Ehmann, 1981).

PLETHOLAX (Figs 2F, 3F). The jaw is long and slender, but with a well-developed dorsal process of the coronoid. Tooth counts are below 20 (Kluge, 1976), with the mesial teeth relatively robust, pointed and slightly recurved while the more distal teeth are markedly reduced in size. The splenial is reduced to a narrow splint but still encloses the inferior alveolar foramen and forms the dorsal margin of the anterior mylohyoid foramen. There is a single posterior surangular foramen. Shea & Peterson (1993) found that most guts of this species contained little chitinous material but often included short cut lengths of grass, consistent with digestion from the bodies of insect prey. They suggested the most likely diet was poorly-sclerotised, readily digested prey such as termites. Ehmann (1993) suggested that *Pletholax* is a nectar feeder. The weak jaws and small, widely spaced teeth suggest it would be unlikely to deal effectively with the tough exoskeletons of typical invertebrate prey.

APRASIA (Figs 2G, 3G). The mandible has only 3 elements; dentary, coronoid and a compound bone representing the remainder; the splenial is absent, whether through loss or fusion is unclear. The inferior alveolar foramen lies on the suture between the anterior extremity of the compound bone and the dentary. The posterior surangular foramen is single. The dorsal process of the

coronoid is reduced and the retroarticular process is abbreviated. The teeth are very greatly reduced in number, restricted to a patch of 3-4 relatively robust, pointed, recurved teeth situated close to (but not on) the symphysis. The diet is restricted to the eggs, larvae and pupae of ants (Webb & Shine, 1994). The mandibular and dental anatomy of *Aprasia* is thus convergent to some extent on that of ant-eating scolecophidian snakes, which also have weak, almost edentulous jaws save for a few teeth in the upper (Typhlopidae) or lower (Leptotyphlopidae) mandible.

LIALIS (Figs 2H, 3H). This genus has a highly derived mandibular morphology. The dentary is greatly attenuated, with many (to over 60) small, recurved, sharply pointed teeth having ligamentous basal attachments (*L. burtonis*, Patchell & Shine, 1986b; *L. jicari*, G. Shea, pers. comm.). Other peculiarities include the greatly reduced height of the coronoid and a peculiar fan-like medial articular process of the surangular ascending well above the level of the articular region, and higher than the coronoid. Functionally this braces the jaw against the quadrate ramus of the pterygoid, preventing lateral displacement of the jaw when the mouth is open. Along with these apomorphies, *Lialis* retains a plesiomorphic, relatively large, anteriorly extending splenial. The posterior surangular foramen is single or double. The wide gape and specialised dentition are related to the obligate lizard-eating (especially skink-eating) habits of this genus (Patchell & Shine, 1986b).

SYSTEMATICS

Infraorder GEKKOTA Cuvier, 1817
Family PYGOPODIDAE

Pygopus Merrem, 1870

TYPE SPECIES. *Bipes lepidopodus* Lacepede, 1804

Pygopus hortulanus sp. nov. (Figs)

ETYMOLOGY. Latin *hortulanus*, of or belonging to a garden; alluding to the Neville's Garden Site.

MATERIAL. Holotype QMF16875 (Fig. 4), a right dentary preserving the complete tooth row and symphyseal region but minus the angular process from early Miocene, System B (Archer et al., 1994), Neville's Garden Site on D Site Plateau at Riversleigh, NW Queensland; the site is interpreted as representing an accumulation in a pool close to a cave entrance.

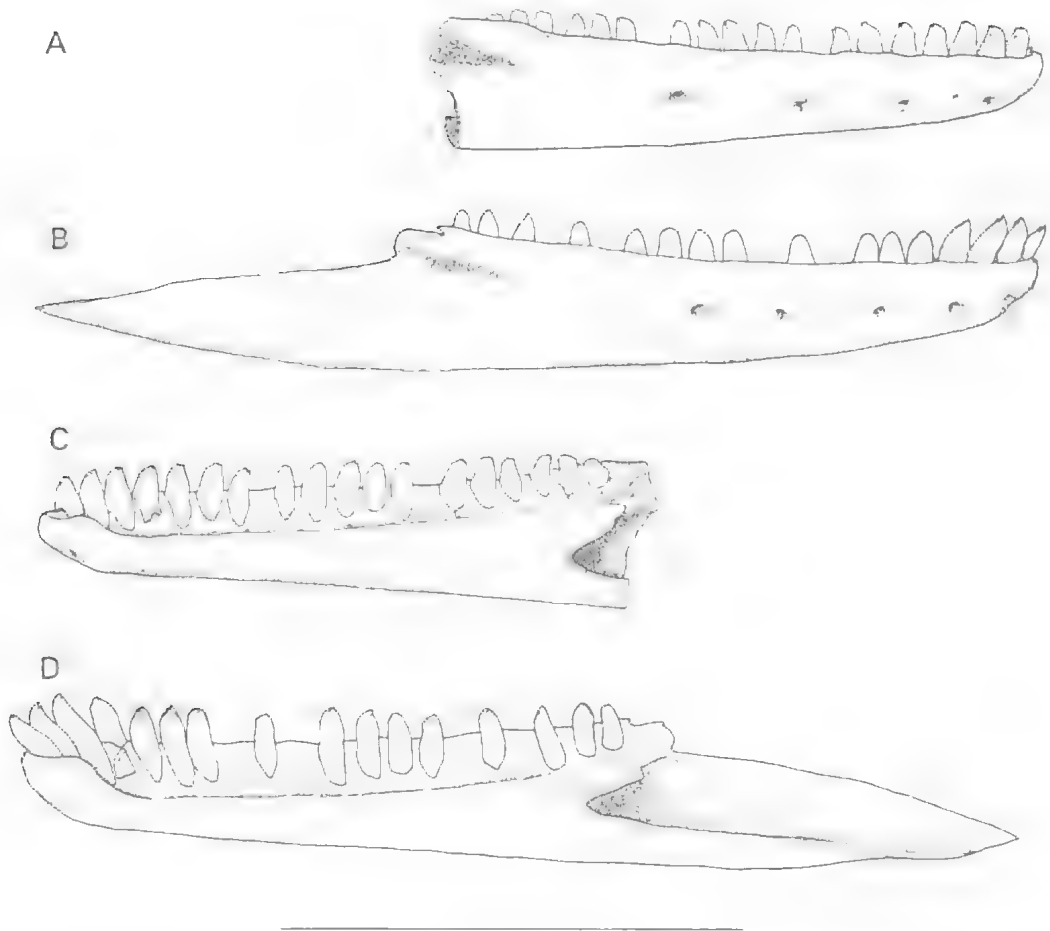


FIG. 4 Comparison of the dentaries of *Pygopus hortulanus* SP. NOV. (A and C, QMF16785) and *P. lepidopodus* (B and D; SAMAR38928). A-B, labial views; C-D, lingual views. Note larger mesial (anteriormost) teeth and deeper symphysis in *P. lepidopodus*. Scale=5mm.

DESCRIPTION. Right dentary, complete and undamaged except for the absence of the angular process posterior to the level of the end of the tooth row. Dental arcade in occlusal view straight from distal tooth anteriorly to about seventh tooth (counting mesiodistally), then curving gently mesially. Lingual rim of dental sulcus distinct, rounded in cross-section. Groove for Meckel's cartilage completely obliterated by overgrowth of dentary. Intramandibular septum not extended posteriorly. In labial view, acute-angled splenial notch extending to level of penultimate (twentieth) tooth, and superficial facet for anterior extension of splenial extending as far as seventeenth tooth. Wedge-shaped facet for anteroventral extremity of coronoid incised into posterior margin between dorsal edge of splenial notch and last

tooth. Labial surface with 5 mental foramina, last level with fourteenth tooth. Shallow fossa on labial surface tapering anteriorly from posterodorsal margin of dentary. Total length 6.0mm; depth at level of last tooth 1.4mm (tooth excluded).

Tooth loci 21. Counting from mesial to distal, all but first (broken), ninth and fifteenth (empty) with intact teeth. Twentieth tooth lost subsequent to preparation of Fig. 4. Length of tooth row 5.2mm.

Teeth robust, 2.5-3 times as high as wide, crowns tapering rapidly to sharp points. Well-defined groove traversing each tooth crown, setting off weak second apical point, lower and lingual to main tooth apex. Tooth crowns slightly incurved. Teeth reducing gradually in size from

mesial to distal, but anteriormost teeth only slightly larger than mid-dentary teeth.

REMARKS. Identification of the fossil as a gekkonoid is based on apomorphic features: 1) obliteration of the groove for Meckel's cartilage by overgrowth of the dentary, 2) apex of the splenial notch level with the posterior end of the tooth row, with a narrow tongue of the splenial extending forward over the lingual face of the dentary below the tooth row, and 3) mesial (i.e. anteriormost) teeth largest (rather than mid-dentary teeth).

Many Australian skinks (Scincidae) also have the Meckelian groove obliterated by the dentary, but in these the splenial notch extends well forward under the tooth row (the tiny *Notoscincus*, tooth row <3mm, is an exception), and scincid dentaries with a closed Meckel's groove all have a vertically oriented, posteriorly extended intramandibular septum. Skinks, unlike gekkonoids (Bauer, 1990; Bauer & Russell, 1990), have the mid-dentary teeth larger than the mesial teeth. Scincid dentaries also have a pronounced coronoid process on the labial surface (Estes, 1983); although this part of the specimen is incomplete, existing outlines indicate that very little of this region is lost and that there was scarcely any development of this process. The only other lizard families in which dentary obliteration of the Meckelian groove occurs are the Xantusiidae (all), many Gymnophthalmidae and many iguanians (Presch, 1980; Estes et al., 1988; Etheridge & de Queiroz, 1988; MacLean, 1974). These can be excluded on the basis of tooth crown shape (McDowell & Bogert, 1954; Sumida & Murphy, 1987; MacLean, 1974; Etheridge & de Queiroz, 1988), and having mid-dentary teeth larger than mesial teeth.

Among gekkonoids, only pygopods have the stout, straight dentary shape, low dentary tooth counts and teeth of the robust form seen in *P. hortulanus*.

Pygopus hortulanus shows two seemingly derived character states within pygopods, the relatively short, deep dentary and the fewer robust teeth. These relate it not only to *Pygopus* but also *Ophidiocephalus*. The fossil is plesiomorphic with respect to *Ophidiocephalus* in straighter tooth crowns, more teeth and greater anterior extent of the splenial. It is plesiomorphic with respect to *Pygopus* perhaps in the less enlarged mesial teeth and (?correlated) shallower symphyseal region. Alternatively the more even tooth row of *P. hortulanus* could be interpreted as

autapomorphic, because enlarged anterior teeth are common in pygopods. The placement of the species in *Pygopus* rather than *Ophidiocephalus* reflects the fewer specialisations shared with *Ophidiocephalus* than with *Pygopus*.

The cladistic analysis of intergeneric relationships reported by Kluge (1974, 1976) not only concluded that *Pygopus* is the most primitive extant genus but also placed *Pygopus* as a grade group at the base of the pygopod radiation and suggested that *Paradelma orientalis* is more closely related to *Pygopus nigriceps* than the latter is to *Py. lepidopodus*. The placement of the fossil in *Pygopus* could therefore be taken to mean only that the fossil is a plesiomorphic pygopod. However, the short, deep dentary and robust teeth of *Pygopus* are probably apomorphic in pygopods, and I therefore maintain the concept of this genus employed by Cogger (1985), Greer (1989) and Shea (1993).

This early Miocene pygopod is consistent with Kluge's (1987) suggestion that pygopods evolved on the Australian continent subsequent to a Late Cretaceous vicariant event isolating the ancestral diplodactyline-pygopod stock. This find, with its apomorphic teeth, is not a generalised ancestral pygopod, implying the origins of the group must be older than the Miocene.

Archer et al. (1989, 1995) suggested that the Miocene environment of Riversleigh was primarily tropical closed forest, an assessment supported by many genera in Systems B and C whose living representatives are restricted to closed forest environments. Megirian (1992) suggested that sedimentological evidence argued for a more arid climate with any rainforest limited to water courses. Creaser (this volume) reports that sediment patterns regarded by Megirian as being confined to arid depositional environments occur today in mid-montane New Guinea.

No modern pygopod inhabits rainforest, although *Lialis* and some *Delma* (Shea, 1987) inhabit vine scrubs and eucalypt forest on the margins of rainforest. The presence of *P. hortulanus* in System B could be interpreted to indicate either that there were drier, open patches nearby, or that *P. hortulanus* was a rainforest-dweller with no living analogue.

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APPENDIX

Pygopodid skeletal specimens examined: *Achlys concinna* SAMA R38060; *Aprasia inaurita* SAMA R14275; *A. pseudopulchella* SAMA R406A; *A. striolata* SAMA R35569, R41825; *Aprasia* sp. SAMA unregistered alizarin specimen; *Delma australis* SAMA R15958; *D. butleri* SAMA R14913, R16843A; *D. fraseri* SAMA R22911; *D. impar* NMV D15446; *D. inornata* SAMA R22408, R35570, NMV D15448; *D. mitella* AMS R65264 (partial dentary only); *D. molleri* SAMA R22540, R35572; *D. nasuta* SAMA R22517; *D. plebeia* QM J5891; *D. tinia* SAMA R15189A; *Lialis burtonis* SAMA R15882, R40031, QM J47481, NMV D15399; *L. jicari* SAMA R11441; *Ophidiocephalus*

taeniatus SAMA R28365 (mandible only);
Paradelma orientalis QM J30250 (mandible
only); *Pletholax gracilis* SAMA R38061;
Pygopus lepidopodus SAMA R19604 (mandible
only), R35571, R38924-28; *P. nigriceps* SAMA
R1250, R21029.

TWO NEW EARLY MIOCENE THYLACINES FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

JEANETTE MUIRHEAD

Muirhead, J. 1997 06 30: Two new early Miocene thylacines from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 367-377. Brisbane. ISSN 0079-8835.

Thylacines, *Wabulacinus ridei* gen. et sp. nov. and *Ngamalacinus turnnallvaneyi* gen. et sp. nov., are described from the early Miocene of Riversleigh, northwestern Queensland. Both show carnivorous adaptation intermediate between that of the plesiomorphic *Nimbacinus dicksoni* and derived *Thylacinus*. The family concept is revised to include these new taxa. All known thylacinid genera occur in late Oligocene to middle Miocene Riversleigh faunas and some may have overlapped in time followed by a decline in family diversity since the Miocene. □ *Thylacine, marsupial, carnivore, Miocene, Riversleigh, Queensland.*

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The Thylacinidae consists of three species of *Thylacinus* (*T. cynocephalus* Harris, 1808, *T. potens* Woodburne, 1967 and *T. macknessi* Muirhead, 1992) and the monotypic *Nimbacinus dicksoni* Muirhead & Archer, 1990 from the late Oligocene to middle Miocene of Queensland and the Northern Territory (Muirhead & Archer, 1990). It is the oldest and most primitive thylacinid, more closely resembling dasyurids in many plesiomorphic features. *Thylacinus potens* from the late Miocene Alcoota Local Fauna (Woodburne, 1967) is considered (Archer, 1982) the sister species of modern *T. cynocephalus* and is almost as specialised. *Thylacinus macknessi*, from early to middle Miocene Riversleigh faunas, is also a highly specialised thylacine. Because it retains some plesiomorphic features, it is considered to be the sister species to the *T. potens*-*T. cynocephalus* clade (Muirhead, 1992). Two new early Miocene thylacinids from Riversleigh are described here. In many features they provide a continuum in morphological change from the plesiomorphic dentition of *N. dicksoni* to that of specialised *Thylacinus*. Dental nomenclature follows Flower (1869) and Luckett (1993) where the adult dentition includes P1-3 and M1-4. Taxonomic nomenclature follows Muirhead & Archer (1990). Material is housed in the Queensland Museum (QMF) or Northern Territory Museum.

SYSTEMATICS

Order DASYUROMORPHIA (Gill, 1872)
Superfamily DASYUROIDEA (Goldfuss, 1820)
Family THYLACINIDAE (Bonaparte, 1838)

Wabulacinus gen. nov.

TYPE SPECIES. *Wabulacinus ridei* gen. et sp. nov.

ETYMOLOGY. Wanyii *Wabula*, long ago; Greek *kynos*, dog. Masculine.

DIAGNOSIS. Infraorbital foramen surrounded wholly by the maxillary and positioned low and anterior to M¹; centrocrista and preparacrista parallel, forming continuous straight line on M¹; entoconid absent (on M₃); hypoconulid enlarged (on M₃).

COMPARISON. *Wabulacinus* differ from *N. dicksoni* by larger size, lack of styler cusps B and D on M¹, lack of styler cusp B on M² and the minute size of St D on this tooth, the straight or almost straight centrocrista on M¹ and M², anterior cingulum of M¹ has no notch for placement of preceding premolar, the anterior root of M¹ lies directly under the cingulum, the anterior width of the upper molar crowns are less than that of the buccal lengths, wider angle of crests at the paracone and metacone, extreme reduction of the talonid basin and protocone, particularly on M¹ with concurrent loss of metaconules on this tooth, extreme reduction in size of the metaconid, absence of entoconid, reduced talonid basin by the more lingual position of the hypoconid and lack of diastemata between P₁ and P₂.

Species of *Wabulacinus* differ from all species of *Thylacinus* in the extreme reduction of the talon and protocone on M¹, the more parallel alignment of the preparacrista with the centrocrista on M¹, a small metaconid (at least on the M₃), less elongate snout by lack of diastemata between the premolars as well as between P₁ and the canine. *Wabulacinus ridei* is similar in molar

size to *T. macknessi*, but lacks an anterior cingulum on M^1 .

***Wabulacinus ridei* sp. nov.**
(Fig. 1)

ETYMOLOGY. For David Ride for his long-term commitment to Australian vertebrate palaeontology.

MATERIAL. Holotype. QMF16851, right maxillary fragment containing M^{1-2} (Fig. 1A-C). Paratype. QMF16852 left dentary fragment with broken M_3 (Fig. 1D-F) from early Miocene (System B) Camel Sputum Site, Godthelp Hill, Riversleigh.

DIAGNOSIS. As for genus.

DESCRIPTION. Maxilla partly preserved. Infraorbital foramen enclosed within the body of maxilla, above the posterior alveolus of P^3 .

Buccal crown of M^1 length exceeds anterior width. Metacone largest cusp followed by paracone, protocone and St E. No other cusps. Postmetacrista longest crest, curving buccally at the posterior end. Preparacrista orientated almost parallel to the tooth row, terminating at the anterior tip of the crown. Premetacrista and postparacrista connecting as a straight centrocrista which parallels the preparacrista. Lacking preprotocrista, postprotocrista, protoconule, metaconule, styler shelf or styler cusps anterior to St E. Buccal flank of crown forming continuous slope from paracone and metacone to lowest buccal edge of the crown. Protocone small.

M^2 similar to M^1 except: St E minute. Styler shelf region high, of many tiny indistinct cusps and crests, especially on the more posterior half of the crown. Postmetacrista longest crest on the crown, followed in declining length by preparacrista, postprotocrista, preprotocrista, postparacrista

and premetacrista. Postparacrista and premetacrista forming a wide angled centrocrista. Postmetacrista leaving metacone almost parallel to the premetacrista, curving buccally. Preparacrista straight, connecting to the postpara-

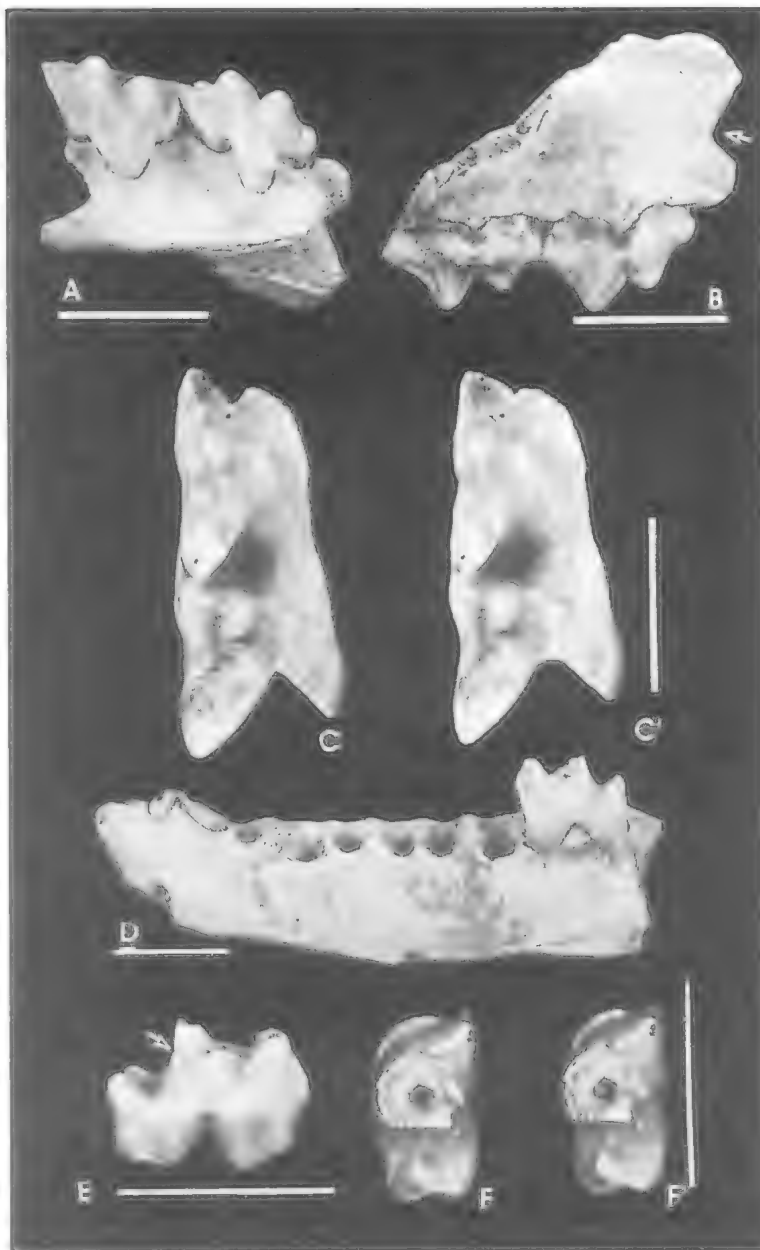


FIG. 1. *Wabulacinus ridei*. A = QMF16851 (M^1 and M^2) lingual view. B = QMF16851 (M^1 and M^2) buccal view with infraorbital foramen arrowed. C and C' = QMF16851 stereo occlusal views. D = QMF16852 (P_2 and M_3) buccal view. E = QMF16852 (M_3) lingual view showing small metaconid (arrowed). F and F' = QMF16852 stereo occlusal view.

crista at approximately 90° and oblique to the tooth row. No St B present. Trigon basin wider than on M¹. Lingual flank of trigon basin 'V'-shaped with a distinct ridge running vertically down its centre. The preprotocrista and postprotocrista prominent with a minute protoconule and metaconule. Ectoflexus on the buccal surface of this tooth slightly developed. Anterior cingulum terminating anterior to base of the paracone, lacking a notch.

Mental foramen under the anterior root of P₂. Alveoli for P₁₋₃, M₁₋₂ and the anterior root of M₃; M₃ only molar present. Symphysis beginning adjacent to the anterior root of P₃. No diastemata between alveoli. All alveoli pairs orientated parallel to the tooth row except P₁ oblique, indicating some crowding of P₁ against the canine. Alveoli size indicating relative lengths of P₃ > P₂ > P₁, M₃ = M₂ > M₁.

M₁ with cusps in decreasing height paraconid, metaconid, hypoconulid, hypoconid. All cusps prominent except minute metaconid; entoconid and related crests absent. Protocristid longest crest, followed (in decreasing length) by the posthypoecristid and cristid obliqua. Remains of the metaecristid connect to the small metaconid. Small talonid basin open on the lingual side. Hypoconid almost medial to the trigonid basin. Posthypoecristid and cristid obliqua orientated oblique to the dentary, meeting at the hypoconid at right angles. Anterior cingulum continuing buccally past the anterobuccal corner of tooth, with wide notch. Posterior cingulum poorly developed, a small bulge in the enamel.

Ngamalacinus gen. nov.

TYPE SPECIES. *Ngamalacinus timmulvaneyi* et sp. nov.

ETYMOLOGY. Wanyii *Ngamala*, died out; Greek *lynos*, dog, Masculine.

DIAGNOSIS. Moderately specialised among thylacinids in the reduced conules, reduced stylar shelf, anteroposteriorly elongated molars. Retaining small St B and D, metaconid, entoconid and hypoconulid.

COMPARISON. *Ngamalacinus* differs from *N. dicksoni* in its larger size, reduced metaconules and protoconules, reduction of St D particularly on M².

Ngamalacinus differs from *W. ridei* and *Thylacinus* in its: smaller size; narrower angle of crests at the paracone, metacone and protocone;

narrower angle of centrocrista; less reduced stylar shelf with retention of prominent St B, St D and stylar shelf crests on M¹ and M²; less reduced talon basin, particularly on M¹; less anteroposterior elongation of the molars and associated crest lengths; larger talonids; and larger metaconid (larger than the paraconid) and with a distinct metaecristid.

Ngamalacinus further differs from *W. ridei* in the more posterior position of the infraorbital foramen, presence of an entoconid on the lower molars and smaller hypoconulid.

Ngamalacinus timmulvaneyi sp. nov. (Figs 2, 3)

ETYMOLOGY. For Tim Mulvaney, a long-time supporter of research at Riversleigh.

MATERIAL. Holotype QMF16853 right dentary with M₁₋₃ (Fig. 2) from early Miocene (System B) Inakeyance Site, Godthelp Hill, Riversleigh. Paratypes QMF30300 left maxillary with P₂-M₃ (Fig. 3A-C), from early Miocene (System B) Camel Sputum Site, Godthelp Hill. Referred specimen QMF16855, right M² (Fig. 3D), from the type locality.

DIAGNOSIS. As for genus.

DESCRIPTION. All articulating surfaces of dentary broken. Coronoid process rising from the ramus at approximately 120°. All four molars and the posterior alveolus of P³ present. No diastemata between these teeth. Degree of eruption of M₁ indicating a juvenile.

Protoconid of M₁ tallest cusp, followed (in decreasing height) by metaconid, paraconid, hypoconid, hypoconulid and entoconid. All cusps distinct, with crests. Paracristid longest crest on crown followed (in decreasing length) by posthypoecristid, metaecristid, cristid obliqua, pre-, postentocristid. Anterior cingulum with a very small notch. Paracristid almost straight with a very wide angle connecting the paraconid and protoconid. Talonid basin entirely enclosed by crests, large and deeply concave to central point. Hypoconid more buccally positioned than protoconid. Cristid obliqua continuing up the posterior wall of the protoconid. Posterior cingulum distinct, uniform in thickness to the base of the crown, with a slight notch formed between it and the hypoconulid.

M₂ same as M₁ except Metaconid relatively large, distinct, taller than the paraconid. All cristids higher and distinct. Anterior cingulum broader and the notch more distinct. Angle at crests on the protoconid approximately 100-110°.

Paracristid and metacristid longer. Metacristid straight; paracristid changing orientation at the valley between the paraconid and protoconid.

M₃ same as M₂ except: the anterior half of the crown thicker than the posterior because of the more lingual position of the paraconid and metaconid. Paracristid and metacristid elongated. Hypoconulid and entoconid slightly more to posterior, with entoconid slightly smaller than on M₂. Posthypoconid bending posteriorly to connect to the posteriorly positioned hypoconulid. Paracristid proportionally longer than on M₂.

M₄ same as M₃ except: Talonid basin reduced, well defined and enclosed by crests. Entoconid minute; hypoconid small; hypoconulid highest cusp on talonid. Small posterior cingulum present.

No obvious sutural boundaries on the maxilla except a posterior suture that may have connected to either the jugal or the lachrymal. Maxilla indicating that the canine was large, its root extending deeply into the maxilla. Infraorbital foramen above M₂. The region immediately posterior to the infraorbital foramen damaged but a depression in the maxilla here and sutural boundaries of the jugal indicate that the jugal is likely to have contacted the external opening of the infraorbital canal. Maxilla with large extension projecting back towards and contributing to the zygomatic arch. No maxillary palatal vacuities in the region of the premolars.

Small diastemata between the upper premolars. P² triangular in lateral view with both an anterior and posterior cusp, with a crest from the major central cusp to the posterior cusp and a less well defined crest anteriorly to the smaller anterior cusp, with posterior region wider than the anterior, with ridges extending along both sides (lingual and buccal) of the posterior cusp. P³ larger than P² and similar except for: anterior and posterior cusps relatively larger, anterior cusp with ridges off the lingual and buccal sides, posterior crest from the major cusp more prominent but not straight, posterior half of tooth relatively wider with enlarged crests bordering the posterolingual and posterobuccal edges of the crown, with an additional posterobuccal cusp.

M¹ damaged, with anterior cingulum, a large St D larger than the distinct St B, a stylar crest running posteriorly from St D to the metastylar corner, talon broad with a possible protoconule, postmetacrista long and straight, crests at the paracone at approximately 90°, preparacrista connecting to St B, almost perpendicular to the tooth row.

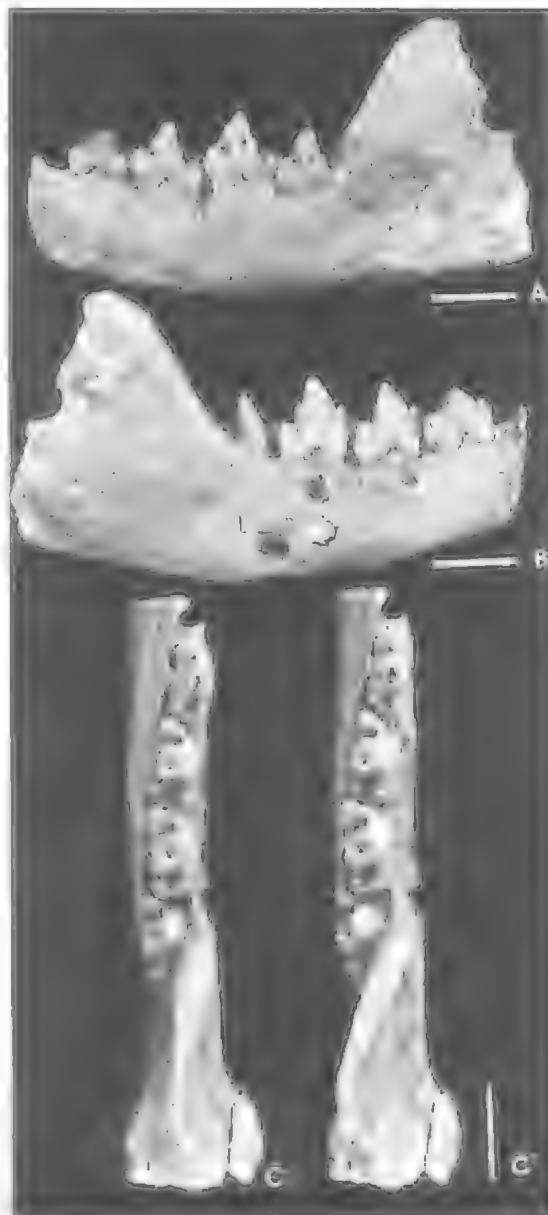


FIG. 2. *Ngamalacinus timmulvaneyi* lower dentition. A = QMF16853 (dentary with M₁₋₅) lingual view. B = QMF16853 buccal view. C and C' = QMF16853

M² same as M¹ with: in occlusal view posterolingual dimension longest followed by buccal length and anterior width. Anterior cingulum not notched in QMF16855 but is in QMF30300, cingulum terminating at the anterior face of the base of the paracone without connecting to the talon basin. No posterior cingulum. Metacone highest cusp on the crown, followed (in

decreasing height) by: paracone, St B, metastylar cusp(s) and protocone. Postmetacrista longest crest on the crown, followed by the preparacrista, premetacrista, postprotocrista, preprotocrista and postparacrista. All crests relatively straight. Enamel surface slightly raised about the protoconule. Metaconule not present as a distinct cusp. Slightly raised postprotocrista connecting the protocone to the metacone base where a sharp crest runs up the lingual surface of the metacone. A less distinct ridge running down the lingual side of the paracone and protocone. Slight ectoflexus at the buccal side of the crown due to bulging of enamel around St B. St E a raised part of the stylar crest. Between St E and B are minute cusps on QMF16855 but St D is more distinct on QMF30300. One crest connecting the metastylar cusp(s) to the posterolingual corner of the crown. Talon basin large with a broad, flat base. Preprotocrista and postprotocrista relatively low. Centrocrista at approximately 100° .

M³ same as M² except: Ectoflexus stronger and all stylar cusps reduced to cuspsules. Stylar crest not continuous along the lingual edge of the crown. St B largest stylar cusp. Anterior cingulum with less distinct notch than in M² of QMF30300. Preparacrista and postmetacrista longer; paracone relatively larger but smaller than metacone. Paracone more lingually located. Centrocrista at approximately 90° ; postparacrista strongly curved. Talon narrower. Protoconule and metaconule with ridges connecting to the lingual face of the paracone and metacone respectively.

THYLACINID PHYLOGENY

Ngamalacinus timmulvaneyi and *W. ridei* do not share any apomorphies that are not also found in *Thylacinus*.

These, therefore, cannot be considered to represent members of the same genus.

Wabulacinus ridei and *Ng. timmulvaneyi* have combinations of features that place them between

plesiomorphic *N. dicksoni* and apomorphic *Thylacinus* but do not form an independent dichotomy (Fig. 4). Neither species can be placed in a known genus because: neither shares any

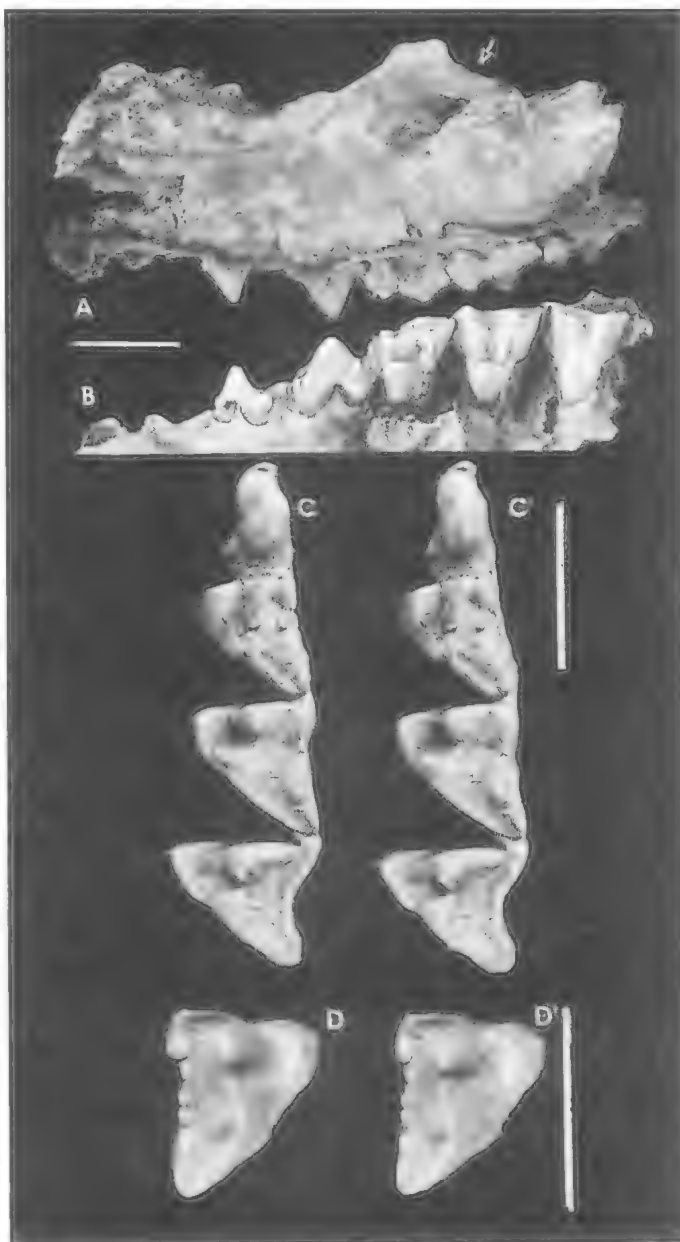


FIG. 3. *Ngamalacinus timmulvaneyi* upper dentition. A = QMF30300 maxillary fragment with P²-M³ and showing infraorbital foramen (arrowed). B and B¹ = QMF30300 stereo occlusal view of P³ and molars. C = QMF30300 lingual view. D and D¹ = QMF16855 (M²) stereo occlusal views.

TABLE 1. Characters and states among thylacines.

1. Infraorbital foramen: 0. not bound by jugal. 1. bound by jugal.
2. Centrocrista. 1. angled. 2. straight (as indicated by M^1).
3. Preparacrista on M^1 . 1. angled almost perpendicular to the tooth row axis. 2. wider angle than state 1. 3. straight.
4. Angle of crests at paracone and metacone. 1. wider than on plesiomorphic dasyurids. 2. further widened.
5. Entoconid. 1. small. 2. minute. a. either absent or posteriorly positioned and combined with the hypoconulid.
6. Hypoconulid size. 0. large. 1. reduced. 2. minute.
7. Styler shelf size. 1. crests and cusps present but reduced compared to plesiomorphic dasyurids. 2. reduction in size of some cusps and crests. 3. further loss of cusps and crests (mostly absent on M^1). 4. complete loss on crests, only a single small cusp present on the posterior of the crown.
8. Anterior cingulum. 0. complete on M^1 . 1. incomplete on M^1 .
9. Metaconule and protoconule. 0. present and large. 1. present and reduced. 2. further reduced or absent.
10. Metaconid size. 1. reduced compared to plesiomorphic dasyurids. 2. small. 3. absent but retention of crest arrangement in posterior molars. 4. complete absence of cusp and associated crests.
11. Talonid basin size. 0. unreduced. 1. reduced by lingual placement of hypoconid. 2. further reduction.
12. Talon size. 1. reduction of talon width compared to plesiomorphic dasyurids with associated lengthening. 2. loss of metaconid and further widening of the crests.
13. Diastemata and size of $M4$. 0. no diastemata in premolar region, $M4$ shorter than $M3$. 1. diastemata and $M4$ equal in length to $M3$. 2. diastemata and $M4$ longer than $M3$.

apomorphy with *N. dicksoni* that is not also shared with *Thylacinus*; to include either in *Thylacinus* would expand it beyond any other dasyuromorphian genus. *Wabulacinus ridei* shows character conflict in the plesiomorphic nature of the infraorbital foramen which is more plesiomorphic than in *N. dicksoni* and *Ng. timmulvaneyi*. This character may have undergone reversal in *W. ridei*.

The single most parsimonious tree of thylacinid relationships was found using an Exhaustive Search PAUP 3.1 (Swofford, 1993) with 13 ordered characters (Tables 1 & 2) using plesiomorphic dasyurids as the outgroup. Each taxon represents the sister species of all thylacines immediately to its right. In general, the

TABLE 2. Character state distribution among thylacines. (a = either 0 or autapomorphic combination of entoconid and hypoconulid, ? = unknown state).

Dasyurids	00000 00000 000
<i>Nimbacinus dicksoni</i>	11111 11001 010
<i>Ngamalacinus timmulvaneyi</i>	11111 12011 010
<i>Wabulacinus ridei</i>	0232a 03112 12?
<i>Thylacinus macknessi</i>	72222 24023 221
<i>Thylacinus potens</i>	12222 24024 222
<i>Thylacinus cynocephalus</i>	12222 24124 222

more specialised carnivores are located on the right.

Wabulacinus ridei and *Ng. timmulvaneyi* are more plesiomorphic than *Thylacinus* in the larger size of the metaconid (small on *W. ridei* and much larger on *Ng. timmulvaneyi*) and the lack of expansion of the premaxillary region. Both species (and particularly *W. ridei*) are more specialised than *N. dicksoni* in the reduction of the styler shelf and the metaconule and protoconule, talon basin and degree of ectoflexus on M^3 .

WABULACINUS RIDEI. Features that are more apomorphic than in *N. dicksoni* and are synapomorphic with *Thylacinus* are: the straight centrocrista; the widened angle of the preparacrista relative to the postparacrista, particularly on the M^1 where this crest is parallel with the anteroposterior dimension of the tooth; an increase in the size of the angle formed by crests at the paracone and metacone, thereby increasing overall tooth length; further reduction in size of the styler cusps than that seen in either *Ng. timmulvaneyi* and *N. dicksoni*; reduction in size of the entoconid; reduction of the metaconid to a minute cusp; reduction in size of the talonid basin by the more lingual position of the hypoconid; and reduction in size of the talon basin.

Wabulacinus ridei exhibits some autapomorphies not seen in any other thylacinid, some of which are considered specialisations beyond that of *T. cynocephalus*. The preparacrista on M^1 of *W. ridei* is parallel with the tooth row and the centrocrista. The preparacristae on *N. dicksoni* and *Ng. timmulvaneyi* show the plesiomorphic state similar to most dasyurids in which it lies almost perpendicular to the tooth row and forms almost a 90° angle with respect to the postparacrista. The morphocline otherwise shown in thylacines from *N. dicksoni* through to *T. cynocephalus* is a widening of the angle at which these crests meet (Fig. 5). This elongates the tooth in an anteroposterior direction and pro-

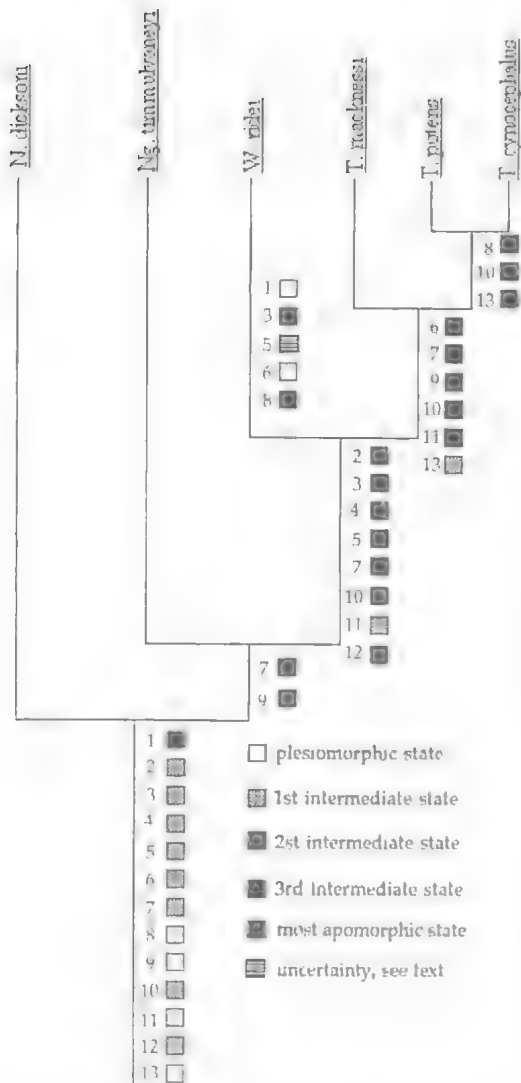


FIG. 4. Cladogram of thylacines showing character state changes. Cladogram is the single most parsimonious tree of 32 steps (CI = 0.906, HI = 0.094, RI = 0.917, RC = 0.831). Striped box = unknown state of either plesiomorphic or highly derived. For characters and their distribution see Tables 1 & 2.

duces an enlarged longitudinal blade formed from the postmetacrista, centrocrista and preparacrista. Only on M^1 of *W. ridei* does the preparacrista lie parallel to the tooth row, a condition more derived than that in any other thylacine. The talon basin on the M^1 of *W. ridei* is also more derived in its degree of reduction than that of *T.*

macknessi but is similar to the condition in *T. cynocephalus*.

The anterior cingulum on M^1 of *W. ridei* is reduced compared to that of *N. dicksoni* (it is unknown in *Ng. timmulvaneyi*). In *W. ridei* it is incomplete while in *N. dicksoni* it continues lingually to join the talon basin. This feature is more plesiomorphic than in *T. cynocephalus* where the cingulum is lost, but more specialised than in *T. macknessi* where a complete cingulum is retained. In addition, the anterior portion of M^1 of *W. ridei* is unique in that the anterior root lies much further forward under the crown than in other thylacines.

Another trend in thylacines is for the entoconid to become reduced. Only in *W. ridei* is this cusp completely lost.

Wabulacinus ridei is autapomorphic within the family in having an enlarged hypoconulid. In other thylacines the hypoconulid shows reduction (e.g., in *N. dicksoni*, *T. cynocephalus*) and may also move posteriorly (e.g., in *T. macknessi*). This enlarged cusp in *W. ridei* may be compensate for loss of the entoconid, or alternatively, it may represent a combination of the hypoconulid and a more posteriorly placed entoconid.

A feature previously used to distinguish thylacines from dasyurids is the posterior position of the infraorbital foramen posteriorly delimited by the jugal (Muirhead & Archer, 1990). It is known in *T. cynocephalus*, *T. potens*, *Ng. timmulvaneyi* (Fig. 3A) and *N. dicksoni*. *Wabulacinus ridei* has the infraorbital foramen anterior to M^1 and well distant from the jugal (Fig. 1B). This position is similar to dasyurids in which it most frequently occurs above M^1/M^2 (e.g., in *Dasyurus* and *Anrechinus*). The anterior position of this foramen in these dasyurids indicates that posterior placement near the jugal in most thylacines is apomorphic (Archer, 1976). The anterior placement of the jugal in *W. ridei* is therefore plesiomorphic relative to other thylacinids.

Wabulacinus ridei is plesiomorphic in many respects to *Thylacinus* excluding it from *Thylacinus*. *W. ridei* has a number of features unique among thylacinids placing it outside the range of variation within *Thylacinus*.

NGAMALACINUS TIMMULVANEYI. This species shares with *W. ridei* and *Thylacinus* the apomorphic reduction in the styler shelf compared to *N. dicksoni* (Fig. 4). This includes reduction in size of St D of M^2 . On QMF16855, St D is further reduced and replaced by a number of minute cusps that border the styler shelf. On other

molars, size of the styler shelf is comparable to that in *N. dicksoni*.

The protoconules and metaconules of *W. ridei* are apomorphically reduced compared to those of *N. dicksoni*. The talon basin is also slightly more reduced than that of *N. dicksoni*. This species further differs from *N. dicksoni* in the less extreme ectoflexus, an apomorphic feature. These specialisations of *Ng. timmulvaneyi* compared to *N. dicksoni* are less marked than the degree of specialisation of these same features in *W. ridei* and *Thylacinus*. *Ngamalacinus timmulvaneyi* and *N. dicksoni* share several plesiomorphies and, in terms of overall similarity, *Ng. timmulvaneyi* is much closer to *N. dicksoni* than to any other thylacinid (Fig. 4). These two species do not share any apomorphy not also found in other thylacines.

PALAEOECOLOGY OF RIVERSLEIGH THYLACINIDS

Thylacinids described from the Riversleigh assemblages are *N. dicksoni*, *Ng. timmulvaneyi*, *W. ridei* and *T. macknessi*. This diversity raises questions about niche diversification. Although only one thylacine appears to have been present at any one time in late Miocene (Alcoota; *T. potens*), Pliocene (Awe & Chinchilla, *T. cynocephalus*) and Quaternary (many assemblages, *T. cynocephalus*) local faunas of Australia and New Guinea (Archer, 1982; Dawson, 1982), prior to the late Miocene, available resources enabled the 'thylacine niche' to be more finely divided. Part of the explanation may be found in the apparent absence from the Riversleigh local faunas of any large dasyurids as specialised for carnivory as the late Cainozoic species of *Glucodon*, *Sarcophilus* and *Dasyurus*. Presence of large carnivorous dasyurids appears inversely correlated with thylacinid diversity. The subsequent rise of these dasyurines may, therefore, have accompanied late Miocene decline in thylacinid diversity.

Although there is a greater diversity of thylacines in the Oligo-Miocene Riversleigh deposits than later, a wider range of large carnivores was also present in these Riversleigh local faunas. For example in single local faunas, there were often 3 crocodilians (P. Willis, pers. comm.), at least 2 large snakes (madtsoiids and pythonids; J. Scanlon, pers. comm.), 2 lineages of thylacoleonids (*Wakaleo* and a genus similar to *Priscileo*; Archer et al., 1989), a possibly carnivorous kangaroo (Archer & Flannery, 1985; Wroe & Archer, 1995; Wroe, 1996) and an unknown

number of raptorial birds (Boles, pers. comm.; Archer et al., 1994). Hence it is probable that the relatively high diversity of Riversleigh thylacines reflects an overall higher biotic diversity in the rainforests of the Riversleigh region.

Camel Sputum is the only Riversleigh site to have produced more than one thylacine: *Ng. timmulvaneyi* and *W. ridei*. These taxa are very similar in size. The maxilla of *Ng. timmulvaneyi* recovered from Camel Sputum Site differs from the maxilla of *W. ridei* in the position of the infraorbital foramen (in *Ng. timmulvaneyi* it typically lies above M² and was probably bounded by the jugal while in *W. ridei* it lies anterior to M¹) and the more plesiomorphic structure of the molars in *Ng. timmulvaneyi*. These differences cannot be accounted for by intraspecific variation and the specimens clearly represent two different species.

It is not clear how many of Riversleigh's thylacines co-existed. While 2 are present in the Camel Sputum assemblage, the more generalised *N. dicksoni* may have been present throughout the Oligo-Miocene (Systems A to C; Muirhead & Archer, 1990). *Thylacinus macknessi* in Systems B and C (Muirhead, 1992) suggests that by the early to middle Miocene, all 4 genera co-existed at Riversleigh. By late Miocene Alcoota time, one lineage is known: *T. potens*.

In late Cainozoic deposits from other areas of Australia (i.e., cave assemblages in eastern, southern and western Australia; Ride, 1964; Archer, 1974, 1982; Dawson, 1982), thylacinid remains are common. Sites where thylacinid remains are abundant (e.g., Thylacine Hole on the Western Australian Nullarbor; Lowry, 1972) may be interpreted to represent lairs or traps where carnivores were preferentially attracted, perhaps by the presence of other animals. In the Riversleigh deposits, most of which appear to have accumulated in shallow pools within rainforest environments (Archer et al., 1989; Archer et al., 1994), thylacinid remains are relatively rare and therefore may more fairly represent natural frequencies.

THYLACINID DIAGNOSIS AND MORPHOLOGICAL TRENDS

Thylacinids differ from dasyurids and other polyprotodont marsupials by having, in combination, the following features. The premetacrista and postparacrista join as a centrocrista. The angle formed by these crests is straight or almost straight in occlusal view in at least M² of the

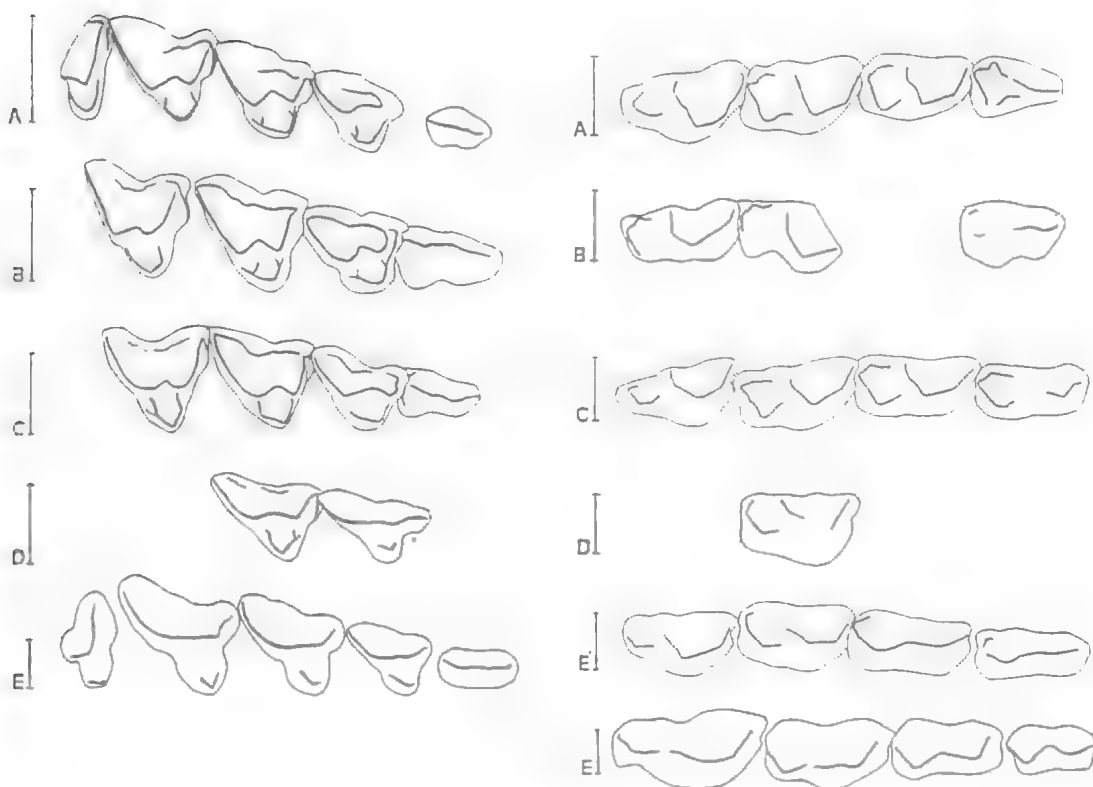


FIG. 5. Upper and lower dentitions of all known thylacine genera showing crest orientation compared to a dasyurid. A=*Dasylurus*. B=*Nimbacinus dicksoni* (P8695-92) C=*Ngamalacinus timmulvanevi*. D=*Wahulacinus ridei*. E¹=*Thylacinus macknessi* E²=*Thylacinus cynocephalus*. Upper dentitions include P³ where known. Scales = 0.5mm.

upper dentition. The cristid obliqua continues up the posterior flank of the protoconid from the talonid region rather than terminating at the base of the protoconid. This functions in elongating this crest and becomes more prominent as the metaconid is reduced (e.g., in *Thylacinus*). The styler cusps are reduced. This occurs most prominently on M³ but also occurs to varying degrees on more anterior molars. The size of the metaconid is reduced on all lower molars. This reduction is correlated with the more posterior placement of the metaconid relative to the protoconid, functioning in widening the angle of crests at the protoconid and enlarging the trigonid basin. Reduction of the metaconid is also found to progress in degree from the more reduced condition on anterior molars to posterior molars (Muirhead & Gillespie, 1995). The size of the talonid basin is reduced because of the more lingual position of the hypoconid. This cusp oc-

cupies much of the surface of the talonid basin such that no flat surfaces occur on the basin floor.

Structural morphoclines of the family (apparent in more specialised forms) include the following. There is an increase in the angles formed by crests of the paracone and metacone, increasing the length of the postmetacrista. More anteroposterior orientation of the preparacrista. The loss of extreme ectoflexus particularly in M³ (related to the overall elongation of the teeth). A reduction in size of the protoconule and metaconule as well as the entire talon basin and reduction in size of the styler shelf. All of these features of the upper dentition increase the anteroposterior length of the molars with the entire tooth row acting as a system of anteroposteriorly orientated blades (Fig. 5). These are typical specialisations in mammalian carnivores.

In the lower molars, the trends are for complete loss of the metaconid and opening of the trigonid

basin. Here, like the upper molars, the lower molar crests become orientated anteroposteriorly (Fig. 5). The paracristid becomes the anterior crest with the elongated cristid obliqua functioning as the posterior crest (the postprotocrista) (Muirhead and Gillespie, 1995). The lingual side of the talonid is also reduced through reduction of the entoconid.

Only in *Thylacinus* is the snout elongated by both diastemata between the canine and premolars and elongation of M4 (such that it is longer than preceding molars). Extreme posterior placement of the infraorbital foramen and partial enclosure by the jugal is also a possible synapomorphy of *Thylacinus* related to snout elongation.

All thylacinids plesiomorphically retain the paraconid on M1, remnants of posterior and anterior cingula on the lower molars and posterior increase in size from P1 to P3.

Variation among thylacinids that does not appear to follow these 'carnivorous trends' includes position of the infraorbital foramen which, plesiomorphically and unlike all other known thylacinids, is more anteriorly positioned in *W. ridgelyi* above P3.

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APPENDIX

All measurements are actual distance between cusps except those with '(horiz)' for which measurements were made from a horizontal plane above the cusps (occlusal view).

Wabulacinus ridei dentition (mm)						
QMF16851			M ¹	M ²		
QMF16852					M ₃	
Para-meta			3.56	3.59	5.06	
Meta-para			4.20	5.01	-	
Proto-para			2.64	3.53	-	
Anterior/width			5.20	6.60	5.20	
Buccal/length			9.00	8.92	9.40	
Posterolingual /uppers			7.37	8.36	-	
para-meta (horiz)			2.90	3.40	4.36	
meta-para (horiz)			2.35	3.55	-	
proto-para (horiz)			2.35	2.85	-	
hypo-hypoconulid			-	-	-	
hyp-ento			-	-	1.81'	
Ngamalacinus timmulvaneyi upper dentition (mm)						
QMF30300	P ²	P ³	M ¹		M ²	
QMF16855				M ²		M ³
Para-meta			3.64	3.66	3.34	3.03
Meta-para			2.86	3.36	3.65	5.00
Proto-para			3.77	5.14	5.02	5.52
Anterior/width	2.25	4.26	4.90	7.68	7.20	8.25
Buccal/length	5.56	7.92	8.11	9.10	8.76	8.17
Posterolingu /uppers			8.15	10.29	9.30	10.27
para-meta (horiz)			3.30	3.42	3.31	2.80
meta-para (horiz)			2.28	3.05	2.84	3.04
proto-para (horiz)			3.34	3.25	3.35	3.20
Ngamalacinus timmulvaneyi lower dentition (mm)						
QMF16853	M ₁		M ₂		M ₃	M ₄
Para-meta	3.56		3.97		4.53	4.37
Meta-para	-		3.09		3.35	3.47
Proto-para	-		4.11		4.92	4.79
Anterior/width	3.34		4.21		4.25	4.78
Buccal/length	7.69		8.37		8.70	8.24
para-meta (horiz)	3.62		3.98		4.50	4.27
meta-para (horiz)	-		2.51		2.64	2.43
proto-para (horiz)	-		3.88		3.89	4.03
hypo-hypoconulid	2.05		2.26		2.10	1.34
hyp-ento	0.76		1.08		1.13	0.90

KUTERINTJA NGAMA (MARSUPIALIA, ILARIIDAE): A REVISED SYSTEMATIC ANALYSIS BASED ON MATERIAL FROM THE LATE OLIGOCENE OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

T.J. MYERS AND M. ARCHER

Myers, T.J. & Archer, M. 1997:06:30. *Kuterintja ngama* (Marsupialia, Ilariidae): a revised systematic analysis based on material from the late Oligocene of Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 379-392. Brisbane. ISSN 0079-8835

The Riversleigh ilariids come from the late Oligocene White Hunter Site and are *Kuterintja ngama* Pledge, 1987. Molar cusp morphologies are compared with those of other ilariids and vombatiforms and several morphoclines identified. The range of variation is similar to that in *Phascolarctos cinereus*. Cladistic analysis suggests several hypotheses about intrafamilial relationships: 1) *Ku. ngama* is an ilariid; 2) *Koobor* is not an ilariid; and 3) ilariids form a monophyletic clade with the wynyardiids, although the relationships of these taxa to other vombatomorphians are not resolved. □ *Ilariidae*, *Oligocene*, *Vombatiformes*, *White Hunter Site*, *Riversleigh*.

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Ilariids are extinct marsupials discovered in late Oligocene deposits of central Australia. *Ilaria* includes *I. illumidens* and *I. lawsoni* (Tedford & Woodburne, 1987); *Kuterintja* contains *Ku. ngama* (Pledge, 1987). There is also some controversy concerning the placement of *Koobor* within the Phascolarctidae because Pledge (1987) suggested that *Ku. ngama* may have been ancestral to *Ko. jimbarratti*, making the latter a potential ilariid. Tedford & Woodburne (1987) found similarities in upper dentition between *I. illumidens* and *Koobor*, namely: a paraconule on M¹, no paraconule or neometaconule on M² or M³, but considered them symplesiomorphic, concluding that *Koobor* shared more synapomorphies with phascolarctids than with ilariids.

We review *Kuterintja ngama* based on material from the White Hunter Local Fauna at Riversleigh, NW Queensland. White Hunter Site on Hal's Hill, on the D-site Plateau (Archer et al., 1994; Creaser, 1997) was questionably assigned to early Miocene System B (Archer et al., 1989, 1994) but the fauna now suggests late Oligocene System A. A tentative correlation is made of White Hunter Local Fauna with the Ngama Local Fauna of the Etadunna Formation at Lake Palankarinna, South Australia.

Pledge (1987) observed that *Kuterintja ngama* differs from *Ilaria* in being smaller, having larger cusps, pre- and posteristae on the styler cusps, postprotocrista and premetaconulecrista separated by a crevice, and an anterior cingulum divided by a stronger preprotocrista. Similarities to *I. illumidens* include a selenodont structure and

well-developed buccal styler cusps. Pledge (1987) described the holotype (SAM P24539) of *Ku. ngama* as a LM⁴. However, material from Riversleigh suggests that the holotype is a LM³.

SYSTEMATICS

Material is deposited in the South Australian Museum (SAMP), and the Queensland Museum (QMF). Homology of molars and the dP₃ follows Lockett (1993). Homology of the other premolars follows Flower (1867). Cusp homology follows Archer (1984). Tedford & Woodburne (1987) and Pledge (1987).

Order DIPROTODONTIA Owen, 1866

Suborder VOMBATIFORMES Woodburne, 1984

Infraorder VOMBATOMORPHIA Aplin & Archer, 1987

Family ILARIIDAE Tedford & Woodburne, 1987

Kuterintja Pledge, 1987

TYPE SPECIES. *Kuterintja ngama* Pledge, 1987 from late Oligocene Etadunna Formation at Lake Palankarinna, northern South Australia.

DIAGNOSIS. Relative to *Ilaria*: Small, lacking transverse linking crests on the cheek teeth. I₁ with low, almost horizontal inclination, dorsally flattened, transversely compressed and with anterior portion inflected.

P₃ subrectangular, with 1 large anterior cuspid and two smaller posterior cuspid only slightly

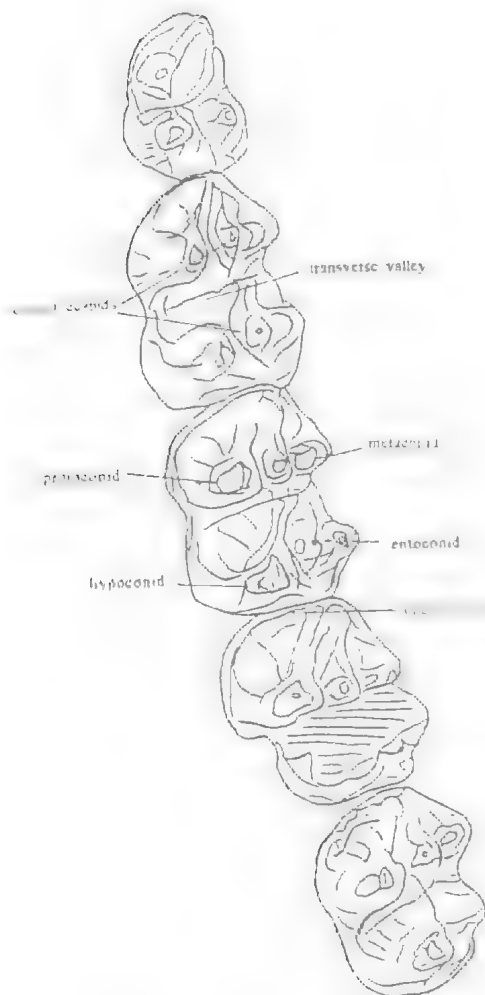


FIG. 1. *Kuterintja ngama*, QMF20810, 23306, left dentary (P₃ - M₄).

separated, one in a posterolingual position, other in a posteromedial position longitudinally aligned with the anterior cuspid. M₁ subovate, with anterior cingulum medially inflected and less developed, with lingual faces of the buccal cuspids near vertical, with less developed preprotocristid and posthypocristid, with preprotocristid and posthypocristid terminating in line with the 'central' cuspids, with small lingual basin on the hypolophid; 'central' cuspid on the protolophid in transverse alignment with the lingual and buccal cuspids on M₁-M₃; metaconid separated slightly from the 'central' cuspid of the protolophid; M₂ with 'central' cuspid on the pro-

tolophid and hypolophid of similar widths and more closely linked, with 'central' cuspid on the hypolophid not linked posteriorly to the entoconid; M₂ and M₃ with preprotocristid and posthypocristid not extending as far lingually; M₃ with lingual basins less developed, with 'central' cuspid on the hypolophid greatly reduced, with posterior cingulum relatively small, with postprotocristid and prehypocristid not blocking transverse valley; M₄ with compressed posterior, with 'central' cuspid not distinguishable on the hypolophid, with the postprotocristid and prehypocristid poorly developed (Fig. 1).

P₃ subovate, much wider both anteriorly and posteriorly compared to the P₃, with narrow anterior portion, with large cusps, tri-cusped, lacking the posterobuccal cusp, with cusps subequal in height, with twinned central cusps separated by a larger trough, with a larger crevice separating posteromedial and posterolingual cusps, with anterolingual cingulum, with well-developed rib running from the apex of posteromedial cusp to the posterobuccal edge of the posterior cingulum.

M₁-₄ with nearly vertical buccal surfaces on cusps. M₁ with stylar cusp C almost as large as the paracone, with stylar cusp D as large as the metacone, with buccal border slanting sharply posterobuccally, with posterior cingulum a round convex structure, with all cusps subequal in height; M₂ with stylar cusp C relatively small, with the cristae forming the borders of the buccal basin on the paracone strongly developed, with the postparacrista separated from stylar cusp C, with stylar cusp E greatly reduced, with preprotocrista strongly developed and dividing the anterior cingulum; M₂ and M₃ with lingual cusps transversely aligned with the buccal cusps; M₂-₄ with the anterior portion of the tooth larger than the posterior; M₃ with stylar cusps B and C equivalent in height to the paracone, with the buccal basin on the paracone enclosed at its buccal margin, with stylar cusp D larger, M₃ and M₄ without stylar cusp E; M₄ with the lingual half of the transverse valley inflected less towards the posterolingual corner, with stylar cusp C variable, with metaconule variable in position, and thus the lingual basin variable in size; (Fig. 4).

COMPARISON: *Kuterintja ngama* differs from phascolarctids in lacking a paraconule and neometaconule, having longer molars, simpler selenes, separation of buccal selenes, better developed stylar cusps, a strongly developed transverse valley, poorly developed postprotocrista and premetaconulecrista, a protocone that is more

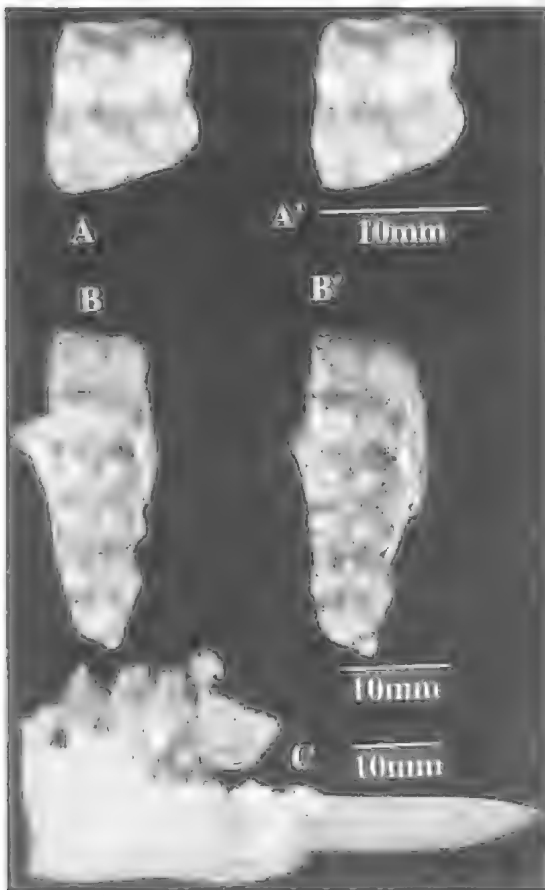


FIG. 2. *Kuterintjangama*. A, QMF30057, RM¹, occlusal view, stereo pair. B, QMF31299, RM²⁻⁴, occlusal view, stereo pair. C, QMF31301, RI¹-M², buccal view.

compressed relative to the metaconule on M¹-M³, significant separation of stylar cusps C and D, no protostylid, a lingually convex metaconid, a protoconid that is larger than the metaconid, lingual cusps that are not compressed towards each other, larger crown height, a well-developed posterolingual cusp on P³, no posterobuccal cusp on P³, central cuspid, having a posterolingual cuspid on P³, a non-bladed P³ or P³, no longitudinal valley, and a bulbous P³.

Ku. ngama is distinguished from *Koobar* by its larger stylar cusps, higher crown, larger molars, and continuous crest between protocone and metaconule (Pledge, 1987). Other differences include: 1) more conical stylar cusps; 2) lower selene angles on the buccal basins of the upper molars; 3) *Koobar* lacks a lingual basin on the transverse valley; 4) *Koobar* has a poorly developed anterior cingulum; 5) the absence of a pos-

terior depression on the metaconule, as exists on most ilariid molars; 6) *Koobar* has molars which are slightly compressed lingually; 7) a much wider and longer longitudinal valley exists in *Koobar*; 8) more poorly developed postproto-crista and premetaconulecrista; 9) a protocone that is compressed longitudinally relative to the metaconule on M¹-M³; 10) no paraconule on M¹; 11) *Koobar* lacks the posterolingual cusp on P³; and 12) *Koobar* has an elongated, rather than bulbous, P³.

Kuterintja ngama Pledge, 1987 (Figs 1-5, 7)

MATERIAL. Holotype SAMP24539, LM³, presumed to be a left M³ by Pledge (1987) from the saddle between Mammalon Hill and main escarpment, NW corner of Lake Palankarina, 100km N of Marree, South Australia in the late Oligocene (Woodburne et al., 1993) Ngama Local Fauna within the Etadunna Formation. Other material. QMF31302, a right dentary fragment containing P³, M¹ and M²; QMF23306, QMF20810, a left dentary with all cheek teeth and the alveoli for I¹; QMF31301, anterior portion of a juvenile right dentary, with I¹, dP³, and M¹. P³ is removed from its crypt, and M² has only part of the protoconid remaining; QMF17527, RM³ with roots missing; QMF31300 RM⁴ with the anterior portion of the trigonid missing; QMF30057, RM¹; QMF23203, LM¹ with a broken anterior cingulum; QMF30058, RM²; QMF31299, right maxillary fragment containing M²⁻⁴; and QMF24604, right maxillary fragment with M³ and M⁴, and alveoli for M¹ and M²; QMF30332, partial right maxilla, with partial palate, anterior zygomatic arch, P³, M² and the alveoli for M¹. All except type from late Oligocene White Hunter Site, Riversleigh, NW Queensland; previously regarded as possibly System A or early System B (Archer et al., 1989; Archer et al. 1994), late Oligocene or early Miocene. This species suggests comparable age to the South Australian type locality.

DIAGNOSIS. As for genus.

DESCRIPTION. Dentary. Deepest below the posterior half of M³. In lateral aspect alveolus for I¹ inclined slightly on its ventral side, horizontal on dorsal side. Mental foramen at the posterior end of this alveolus in the dorsoventral midline, and just anterior to P³, only foramen on the dentary (break dorsoventrally from the junction of M² and M³ may obscure others).

I¹. Lower first incisor projecting horizontally from the dentary, curving lingually at its anterior (distal) extremity, subcylindrical, transversely compressed, with dorsal surface transversely flat-

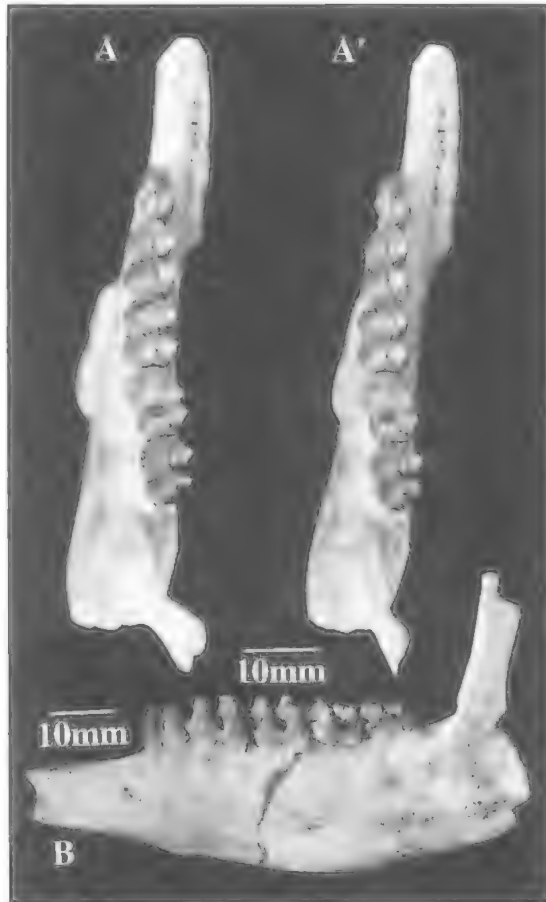


FIG. 3. *Kuterintjangama*. A, QMF20810, left dentary, occlusal view, stereo pair. B, QMF23306, buccal view.

tened, with enamel from the buccal to ventral surfaces.

dP₃. Same as P₃ except in size, tricuspid, sub-triangular.

Anterior cuspid tallest, with widest base. Smaller cuspid posterolingually from anterior cuspid. Third cuspid posterobuccally from anterior cuspid and equivalent in size to the posterolingual cuspid. All cuspids closely linked, conical, with wide bases.

P₃ (Fig. 1). Transversely compressed, tricuspid. Large, subovate, conical cuspid anteriorly larger, taller and more broadly based than the twin cuspids posteriorly. More buccal of these anteroposteriorly aligned with the large, anterior

cuspid. Posterolingual cuspid taller than its worn buccal counterpart.

Thin, low cristid running from the anterolingual corner of the apex of the anterior cuspid, anterolingually to the base of the cuspid, then turning posterolingually and running further down towards the root, then turning posterobuccally up the cuspid and terminating about half way up the height of the cuspid, in line with the posterior side of the apex of the large cuspid. Anterior cuspid located over the posterior portion of the anterior root; posterior cuspids located directly over the posterior root.

A minor crevice on the anterolingual corner of

TABLE 1. Measurements (mm) of dentition of *Kuterintjangama*. Le=length; Mw=maximum width; Ha=height of anterior cuspid; Aw=anterior width; Pw= posterior width; Hp=height of paracone; Hpr=height of protocone; Hm=height of metacone; Hml=height of metaconule; Hprd= height of protoconid; Hmd=height of metaconid; He=height of entoconid; Hh=height of hypoconid. Italicised numbers indicate dimension may have been lessened by wear.

QM No/ID	Le	Mw	Ha	Aw	Pw	Hp	Hpr	Hm	Hml
30332 RP ³	8.9	7.5	4.2	-	-	-	-	-	-
30057 RM ¹	9.7	-	-	8.7	7.7	5.4	4.6	5.2	4.7
31299 RM ²	10	-	-	8.6	8.0	4.8	5.4	4.9	5.1
30058 RM ²	9.4	-	-	8.9	8.8	4.7	5.4	5.1	5.1
30332 RM ²	10	-	-	9.5	9.5	?	?	3.3	3.1
31299 RM ³	8.4	-	-	7.6	6.5	4.4	5.3	4.1	5.1
24604 RM ³	8.5	-	-	8.1	7.0	4.5	5.6	4.4	4.8
31299 RM ⁴	7.2	-	-	6.7	4.9	3.8	4.4	3.3	3.3
24604 RM ⁴	7.6	-	-	6.8	5.5	4.0	5.1	3.4	3.5
23203 LM ¹	10	-	-	8.3	8.0	4.2	4.8	4.2	4.2
31301 dP ₃	3.9	3.6	2.8	-	-	-	-	-	-
31301 RP ₃	6.7	4.9	5.7	-	-	-	-	-	-
31302 RP ₃	6.6	5.0	4.8	-	-	-	-	-	-
31301 RM ₁	10	-	-	6.8	7.4	5.6	5.0	5.7	6.4
31302 RM ₁	9.5	-	-	6.5	7.3	3.7	3.7	4.2	4.0
31301 RM ₂	9.8	-	-	?	?	6.5	?	?	?
31302 RM ₂	9.9	-	-	6.9	7.2	3.8	3.6	4.0	3.7
31301 RM ₃	10	-	-	6.3	5.8	6.0	4.4	4.3	6.1
17527 RM ₃	9.7	-	-	6.4	6.0	6.3	4.4	4.4	6.2
31300 RM ₄	9.1	-	-	?	5.6	3.8	3.5	3.2	3.7
23306 LP ₃	6.8	5.4	5.9	-	-	-	-	-	-
23306 LM ₁	9.9	-	-	6.4	6.9	4.9	4.5	4.7	5.4
23306 LM ₂	9.7	-	-	7.4	7.5	4.9	4.4	4.5	5.1
23306 LM ₃	9.4	-	-	7.2	?	4.4	4.9	4.1	5.0
23306 LM ₄	9.2	-	-	6.8	5.7	4.1	4.2	3.7	3.7

the tooth. A deeper crevice dividing the tooth into sub-equal halves, with the large anterior cuspid on the anterior side and the twinned posterior cusps on the posterior side, blocked half way along by a crest linking the anterior cuspid to the posterobuccal cuspid. A shallower crevice between the posterior cusps blocked by a minor crest running from the apices of these cusps.

Small cristid running posteroventrally from the posterobuccal corner of the apex of the posterobuccal cuspid, turning posterolingually, joining a wider posterior cingulum. Posterior cingulum curving anterolingually before joining the base of the posterolingual cuspid.

Lower Molars. Subrectangular. M₁₋₃ subequal; M₄ smaller. Crown heights decreasing from M₁₋₄. Tooth row curving posterolingually (Fig. 1).

M1: 'Central' cusps on the protolophid and hypolophid are neomorphs (Tedford & Woodburne, 1987). 6-cuspid; anterior portion narrower than posterior. Trigonid triangular; anterolingual border inclined posterolingually; anterobuccal border of trigonid inclined posterobuccally; both these inflections originating from an anteromedial position of the anterior cingulum, at termination of preprotocristid. Talonid wider than trigonid. Protoconid over the posterior portion of the anterior root; posterior cusps aligned over the central portion of the posterior root. Preprotocristid (or paracristid) relatively wide, generally low, with pocket between the buccal margin, the anterior cingulum and the anterior face of the protoconid, with smaller and less well defined pocket between the anterior cingulum, the lingual margin of the preprotocristid and the anterior surfaces of the 'central' cuspid and metaconid. 'Central' cuspid of protolophid with apex slightly anterior to the protoconid and metaconid. Anterior positioning of 'central' cuspid or neomorph more exaggerated on the hypolophid. Both 'central' cusps of similar height, lower than main cusps. 'Central' cuspid on protolophid forming a lingual basin with the metaconid, not totally enclosed, with small openings anteriorly and posteriorly. Similar, small basin formed between the 'central' cuspid of the hypolophid and the entoconid, with comparable openings to its counterpart on the protolophid, with anterior opening much smaller.

A deep crevice dividing 'central' cusps from the main buccal cusps, continuous anteroposteriorly, shallower in the central part of the tooth. Transverse valley interrupting this lon-

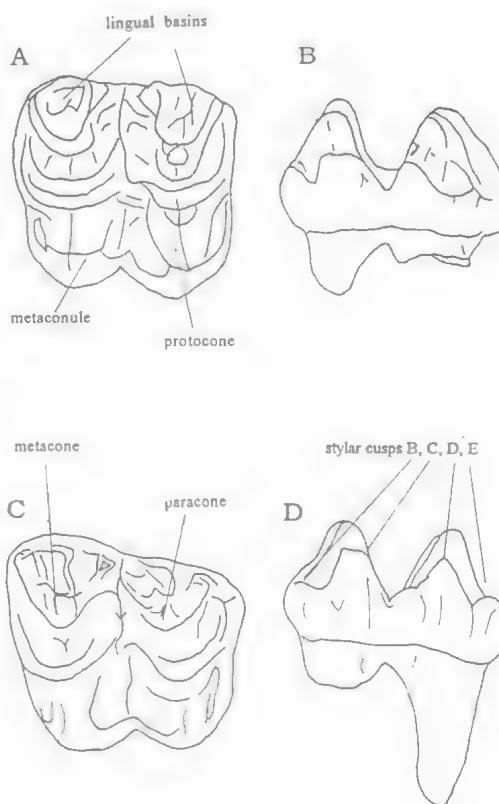


FIG. 4. *Kuterintja ngama*. A-B, QMF30058, RM². A, occlusal view; B, buccal view. C-D, QMF30057, RM¹. C, occlusal view; D, buccal view.

gitudinal crevice wide, blocked at its buccal extremity by a small, posterobuccally slanting cingulum linking the base of the protoconid to the base of the hypoconid. Thin crevice in the transverse valley preventing symmetrical postprotocristid and prehypoconid (cristid obliqua) and postmetacristid and preentocristid from linking. Metaconid and entoconid with apices steeply inclined, rather than conical, with lingual surface of each much taller than the buccal. Entoconid higher than metaconid higher than 'central' cusps, with slight gradient descending from lingual to buccal. A thin posterior cingulum and a small pocket in the posterolingual corner of the tooth; pocket bordered by the lingual end of the posterior cingulum, with 2 crests from the posterolingual and posterobuccal sides of the apex of the entoconid, respectively.

In QMF31301 protoconid and hypoconid with lingual surfaces slightly more vertically orien-

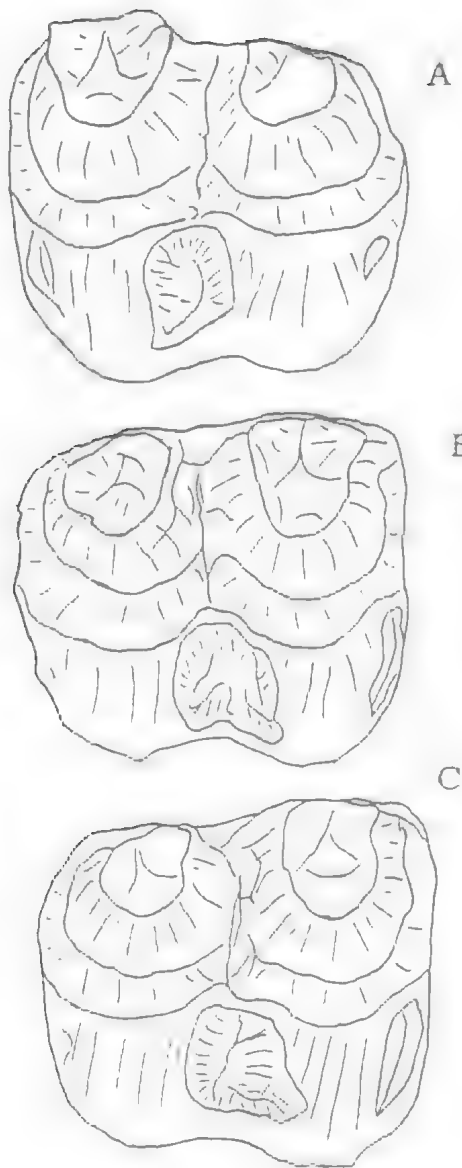


FIG. 5. *Kuterintja ngama*. A, SAMP24539, holotype, LM¹. B, QMF24604, RM¹. C, QMF31299, RM².

tated, possibly due to less wear than observed in QMF23306.

M₂. Like M₁ except: anterior end resting upon the posterior cingulum of M₁; trigonid subrectangular rather than triangular, due to the anterior cingulum being more transversely linear, anterior

pockets formed with the anterior cingulum smaller; trigonid and talonid equal in transverse width. 'Central' cuspid on the protolophid in direct transverse alignment with the protoconid and metaconid; 'central' cuspid on the hypolophid more to anterior; hypoconid slightly more posterior. Crevice between the linked lingual cusps and the buccal cuspid shallower (possibly due to wear on protoconid and hypoconid). Cuspid height gradient from lingual to buccal much steeper (possibly due to wear). Pocket at the buccal end of the transverse valley larger. Cristid obliqua (or prehypocristid) and hypocristid (posthypocristid) more developed. Lingual pocket on the protolophid less well defined, with the openings between the metaconid and 'central' cuspid larger. Small posterolingual pocket bordered by postentoconid, hypocristid and a small posterior cingulum, with most of the latter hidden by M₃.

M₃. Same as M₂ except: anterior cingulum rounded. Crown height reduced; with height gradient. Metaconid and 'central' cuspid not closely linked, separate entities with a crevice between the two cusps. Crevice of variable depth. 'Central' cuspid on the protolophid larger, highlighting an increase in size from M₁ to M₃. Crevice between 'central' and buccal cusps shallower, decreasing in depth down the tooth row. Despite damage to the talonid, 'central' cuspid on the hypolophid much reduced. Entoconid sub-equal in height to the 'central' cuspid on the hypolophid, transversely compressed. Posterior cingulum and posterobuccal basin much shorter.

Juvenile M₃ with an anterolingual basin bigger than in M₁ or M₂, paracristid terminating in longitudinal alignment with the buccal side of the metaconid.

M₄. Shortest and narrowest molar, with lowest crown, rounded subrectangular, with a very rounded anterior cingulum. Same as M₃ except: protolophid and hypolophid slanting more anterolingually, due to the buccal cusps being posterior to the lingual cusps.

'Central' cuspid on the protolophid not linked to the metaconid; crevice between these 2 cusps deeper. 'Central' cuspid on the hypolophid greatly reduced, more so than in M₃, further to posterior. Posterior cingulum short, extending to the medial line of the tooth. Posterolingual basin greatly reduced. Transverse valley closed lingually and buccally. Lingual end of the transverse

valley curving posterolingually; buccal end curving posterobuccally. Cristid obliqua and hypocristid relatively short. All cuspids subequal in height, with the metaconid slightly larger than the entoconid = protoconid and hypoconid.

P^3 . Subovate, tricuspid, transversely wide. Anterior portion narrower than posterior. Cusps 3, large, subequal in height. Anterior and posteromedial cusps longitudinally aligned, separated by a shallow trough. A large crevice separating the posteromedial and posterolingual cusps. With very small anterolingual cingulum and larger posterior cingulum. A thin rib running from the apex of the posteromedial cusp to the posterobuccal edge of the posterior cingulum.

Upper molars. Styler cusps well-developed; general selenodont cusp pattern; high crowned, with a general gradient towards the lingual side, with 4 major cusps (paracone, protocone, metacone and metaconule), with a styler shelf consisting of styler cusps B, C, D and E.

M^1 (Fig. 4). Buccal cusps of RM^1 positioned more posteriorly than in other molars, with posterobuccal slant, wider posteriorly than anteriorly, giving an anterolingual slant to the buccal border. Styler cusp B smaller and further anterior than in other molars. Styler cusp C as large as that on M^2 , anterior to the postparacrista; crista not forming part of the posterior face of the styler cusp. Styler cusp D largest cusp, subequal in height to the metacone, larger than in any other molar. Styler cusp E more developed than in other molars, larger than styler cusp B. A minor cuspule on the anterior of styler cusp D, buccal to the termination of the postmetacrista, larger than styler cusp B, but slightly smaller than styler cusp E. All styler cusps subconical to triangular, except posterobuccally-aligned ridge, styler cusp C. Buccal margin wider than lingual; blocking crests in the transverse valley absent (some minor partial blockages buccally); anterior cingulum curving posterobuccally at its buccal extremity; preparacrista orientated less transversely than in other upper molars; minor depression on the posterior face of the metaconule less developed than in M^2 ; buccal basins on the paracone and metacone poorly developed compared to other molars; posterior cingulum thinner than in other molars.

M^2 (Fig. 4). Square. Cusp sizes: paracone > metacone > protocone = metaconule. Styler

cusp height: $C > D > B > E$. Styler cusp B connected to the paracone by a preparacrista, and styler cusp C via a postparacrista. Styler cusp D connecting to the metacone by a premetacrista, and styler cusp E connected to the metacone by a postmetacrista. Buccal basin deep, formed between styler cusps B and C and the paracone. The homologous basin on the metacone less distinct, enclosed less tightly, slanting steeply posterobuccally towards the reduced styler cusp E. Basin on the metacone deepest anterolingual to styler cusp E. Large transverse valley dividing this tooth in half, containing the paracone (and associated styler cusps) and protocone anteriorly, and the metacone and metaconule posteriorly, partially blocked buccally by an incomplete crest linking premetacrista and postprotoecrista, blocked centrally by a small crest linking postprotoecrista and premetaconule crista, stopped at its lingual extremity by a very low crest linking the lingual sides of protocone and metaconule (lingual cingulum). Buccal faces of protocone and metaconule steeply inclined, almost to the point of being vertical; anterior cingulum well-developed, running buccally from the protoecrista to the anterior side of styler cusp B, and lingually from the anterolingual corner of the base of the protocone to the protoecrista; posterior cingulum smaller than anterior cingulum, with the former extending from styler cusp E to join the postmetaconulecrista; small depression on the lingual side of the postmetaconulecrista and medial posterior base of the metaconule (perhaps remnant of the lingual portion of the posterior cingulum); all cusps over the mid-line of the roots; styler cusps triangular, rather than round or conical; buccal cusps with very round apices.

M^3 (Fig. 5). Same as M^2 except: crown lower, 4 major and styler cusps retaining same relative heights; styler cusp E further reduced, virtually non-existent; posterior cingulum less defined; small pocket on the posterior side of the metaconule on M^2 absent; lingual cusps closer to the anterior side of their respective roots. Styler cusp C more to posterior than in M^2 , with postparacrista forming part of this styler cusp; buccal basin on the paracone of M^3 larger than in M^2 , triangular, with wider buccal edge. Transverse valley partially blocked buccally by a crest linking styler cusps C and D, but not by a crest linking the premetaconulecrista and postparacrista, with central and lingual blocking crests. Crest linking styler cusp D and the metacone larger and more uniform; styler cusp E more

TABLE 2. Characters and character states used in the ilariid intrafamilial phylogenetic analysis.

	Characters	States
1	Stylar cusp development	0=poor; 1=well
2	Transverse valley on lower molars	0=absent; 1=moderate; 2=well-developed
3	Transverse linkages between cuspids	0=none; 1=poor; 2=moderate; 3=well-developed
4	Post protocrista and pre metaconulecrista	0=strongly developed; 1=poorly developed
5	Protocone compressed longitudinally relative to metaconule (on M ¹ -M ²)	0=absent; 1=present
6	Separation of stylar cusps C and D	0=no significant separation; 1=significant separation by large trough
7	Paraconule on M ¹	0=well developed; 1=poorly developed; 2=absent.
8	Paraconid on M ₁	0 = absent; 1= weak; 2 = strongly developed
9	Protostylid	0=present; 1=absent
10	Metaconid	0=conical; 1=lingually convex crest
11	Relative heights of the anterior cuspids	0 = subequal ; 1=protoconid larger than metaconid
12	Overall tooth size	0 =small; 1=large
13	Lingual cusps	0=compressed together; 1=not compressed
14	Crown height	0=low; 1=moderate; 2=high
15	Posterolingual cusp on P ¹	0=absent; 1= slight cusp; 2 = moderate; 3 = well-developed
16	I ₁ (unorderd)	0=dorsoventrally flattened; 1=caniniform and conical; 2=dorsally flattened and distally inflected
17	Posterobuccal cuspid on P ₃	0=absent; 1=present
18	'Central' cuspid	0=absent; 1=present
19	Posterolingual cuspid on P ₃	0=absent; 1=present
20	lingual closure of transverse valley by a cingulum (on upper molars)	0=cingulum absent; 1=incipient cingulum (in form of cuspules); 2=cingulum present
21	Bladed P ₃	0=present; 1=absent
22	Bladed P ³	0=strongly bladed; 1=weakly bladed; 2=absent
23	Posterobuccal cusp on P ³	0=absent; 1=present
24	Longitudinal valley (i.e. distance between lingual & buccal cusps / ids)	0=well-developed; 1=moderately developed; 2=absent
25	P ³	0=bulbous; 1=elongate

anteriorly positioned; buccal basin on the metacone narrower, slanting more anterobuccally.

M⁴. Sub-triangular, posteriorly compressed. Same as M³ except: crown height very small, with the protocone>paracone=metacone>metaconule. Stylar cusp B>D; stylar cusp C non-existent; stylar cusp E extremely reduced or missing. Crevice between the paracone and protocone transversely wider. Buccal surface of the metaconule and protocone far less vertically inclined. Anterobuccal basin larger; buccal basin on the metacone absent; buccal basin on the paracone very shallow, slanting posterobuccally. Transverse valley not blocked buccally, curving posterobuccally rather than being transverse, with lingual end enclosed slightly, by a low crest (i.e. the crest does not continue to the base of the protocone). Anterior cingulum very small. Posterior root slants posteriorly rather than vertically.

REMARKS. Comparing LM¹ QMF23203 to RM¹ QMF30057: buccal half of the anterior cingulum transversely shorter; stylar cusps B and E less developed; cuspule on the anterior face of stylar cusp D absent. M³ of QMF24604 exhibits variation compared to the M³ of QMF31299 as follows: 1) stylar cusp D is larger; 2) the distance between stylar cusps D and E is greater and therefore a bigger buccal basin is found on the metacone; and 3) the medial lingual basin is divided into two sub-basins at its lingual margin by a very small transverse crest.

QMF24604 highlights the variability in M⁴, as follows: posterior half not as compressed as in M⁴ of QMF31299, and therefore has a longer and wider posterior cingulum. Stylar cusp E is much reduced. Therefore the buccal basin on the metacone is also present and it is as deep as the basin on the paracone. Stylar cusp D is also more defined and larger than in M⁴ of QMF31299. The medial lingual basin is smaller. The anterior cingulum extends further lingually to the base of the protocone. The transverse valley is blocked in two places rather than one. It is blocked buccally by a crest linking stylar cusps C and D, and is partially blocked by a small crest linking postparacrista and premetaconulecrista. The crest partially blocking the lingual extremity in QMF31299 is not present. Large stylar cusp C is not present in QMF31299. A well developed and enclosed buccal basin on the paracone is absent in QMF31299.

TABLE 3. Ilariid intrafamilial data matrix as used by PAUP. ? = fossil material missing or status uncertain; a = 1 & 2; b = 0 & 1; c = 0 & 2

Taxa	CHARACTERS AND STATES																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Madakoala</i> spp.	0	0	1	0	0	0	0	2	0	0	0	0	0	0	1	?	1	0	0	c	0	0	0	0	0
<i>P. cinereus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	1	1	0	0
<i>Koobor notabalis</i>	0	?	?	0	0	0	0	?	?	?	?	0	0	0	0	?	?	?	?	1	?	1	0	1	0
<i>Ilaria illumidens</i>	1	2	2	1	1	1	1	2	0	0	0	1	1	2	2	1	1	1	1	2	0	1	0	2	0
<i>Ilaria lawsoni</i>	?	2	2	?	?	?	?	1	1	1	1	1	?	2	?	1	1	1	1	?	1	2	1	2	1
<i>Kuterintja ngama</i>	1	2	1	1	1	1	2	0	1	1	1	0	1	2	3	2	0	1	1	2	1	?	?	2	?
wynvardiids	1	1	3	0	0	1	2	0	1	0	1	0	1	1	a	2	0	0	0	0	1	2	0	2	1

PHYLOGENETIC SYSTEMATICS

Twentyfive dental characters with up to 4 states each (Table 2) were used to develop the data matrix following character argumentation and polarisation (Table 3) for the intrafamilial analysis of ilariids. Three outgroups used to determine polarities are: 1) the modern Koala, *Phascolarctos cinereus*; 2) *Madakoala*; and 3) wynyardiids. The former is the most derived member of a primitive outgroup because the Phascolarctidae is the stem taxon from which the vombatomorphic radiation diverged (Marshall et al., 1990; Aplin & Archer, 1987). *Madakoala devisi* and *Madakoala wellsi* are employed because of the primitive position of *Madakoala* within the phascolarctid radiation (Woodburne et al., 1987). Primitive and derived phascolarctids were used to determine the relationships of species of *Koobor*. Wynyardiids include *Namilamadeta snideri* and *Muramura sp.* and are a closer sister group of the ilariids than the phascolarctids, therefore providing a basis for polarising character states within the Vombatomorpha.

Character optimisation is performed after the character analysis has been completed and the most parsimonious trees found. The two optimisation algorithms used by PAUP are ACCTRAN and DELTRAN. ACCTRAN accelerates the evolutionary transformation of characters so that changes occur at the earliest possible stage on the optimal tree. As far as homoplasy is concerned, this algorithm has the effect of favouring reversal of character states over convergences. DELTRAN delays transformation of characters so that changes occur as far up the optimal tree as possible. This has the effect of favouring convergences over character reversals (Wiley et al., 1991). DELTRAN analyses are favoured here because of the large amount of missing character data in the matrices.

RESULTS. the optimal tree (Fig. 6) has 50 steps; a consistency index (CI) of 0.800; a homoplasy index (HI) of 0.260; a retention index (RI) of 0.778; and a rescaled consistency index (RC) of 0.622. Notably the ingroup (*Koobor notabalis*, *I. lawsoni*, *I. illumidens* and *Kuterintja ngama*) did not form a monophyletic clade. *Ko. notabalis* is sister taxon to the Wynyardiidae, *Ku. ngama*, *I. illumidens* and *I. lawsoni* clade. *Madakoala* and *Phascolarctos cinereus* formed a basal monophyletic clade.

Bootstrap analysis for the most parsimonious tree had the clade excluding phascolarctids and *Koobor* supported 99% of the time. The ilariid clades, excluding and including *Ku. ngama*, occurred 78% and 95% of the time respectively.

Removal of the wynyardiids as an outgroup had no effect on the topology in the optimal tree. A bootstrap analysis on data excluding the wynyardiids found the clade containing *I. illumidens* and *I. lawsoni* to be supported 62% of the time, slightly lower than in the previous analysis. While the clade including all 3 ilariid species was supported on all occasions.

Another method of testing support for the optimal tree is to examine the frequency and topology of the 'next best' trees (Simmons, 1993). PAUP evaluated 945 trees and found one optimal tree of 50 steps. Two trees of length 51 were observed as well as one tree of 52 steps. Neither of the trees of 51 steps in length are considered here as the phyletic relationships presented by each do not represent the phascolarctids as a monophyletic clade. In both cases *Koobor* is intermediate between *Madakoala* spp. and *Phascolarctos cinereus*.

DISCUSSION

Classification of *Ku. ngama* as an ilariid was tentative (Pledge, 1987) and controversy surrounded placement of *Koobor*. Comparison of the

Riversleigh ilariid with species of *Ilaria* and *Kuterintja ngama*, confirms that the Riversleigh animal is indistinguishable from the latter. Dental variation in *Phascolarctos cinereus*, one of *Ku. ngama*'s closest living relatives, suggests that: 1) variation in Riversleigh fossil material is in the range for vombatiform species, and represents only one taxon; and 2) the Riversleigh species is *Ku. ngama*.

DISCUSSION OF THE PHYLOGENETIC ANALYSIS. *Kuterintja ngama* as the sister taxon of a clade containing *Ilaria illumidens* and *Ilaria lawsoni* (Fig. 6), and not united with wynyardiids or *Koobor*, reinforces classification of this animal as an ilariid. Synapomorphies used by DELTRAN to unite ilariids include: 1) a well-developed transverse valley; 2) poorly-developed postparacrista and premetaconulecrista; 3) protocone longitudinally compressed relative to the metaconule on M^1 - M^3 ; 4) large crown height; 5) moderately well-developed posterolingual cusp on P^3 ; 6) closure of the transverse valley on upper molars by a lingual cingulum; 7) a non-bladed and bulbous P^3 ; 8) a non-bladed P_3 and 9) a 'central' cuspid on the protolophid and hypolophid of lower molars. These synapomorphies only apply to the Ilariidae relative to the other taxa used in this analysis, and may prove to be symplesiomorphies when all other vombatomorphian taxa are included. Some of these synapomorphies refer to the upper dentition, which is unknown for *Ilaria lawsoni*. However, the close similarities between the lower dentition of both *Ilaria* species suggests that these synapomorphies will be generically significant when upper dentition for *I. lawsoni* is found. Synapomorphies used by the same algorithm to unite species of *Ilaria* include: 1) moderately well-developed transverse linkages between cuspids; 2) weak paraconid; 3) large tooth size; and 4) transversely compressed, caniniform lower first incisors.

In constructing the most parsimonious tree, 9 characters were found to exhibit some degree of homoplasy. According to DELTRAN moderately well-developed transverse linkages between cuspids is due to convergence between primitive wynyardiids and species of *Ilaria*, with *Kuterintja ngama* with plesiomorphic poorly developed linkages. Conversely, ACCTRAN suggests that moderately well-developed transverse linkages were already a feature of the common wynyardiid/ilariid ancestor, possibly before *Koobor* diverged from the vombatomorphian lin-

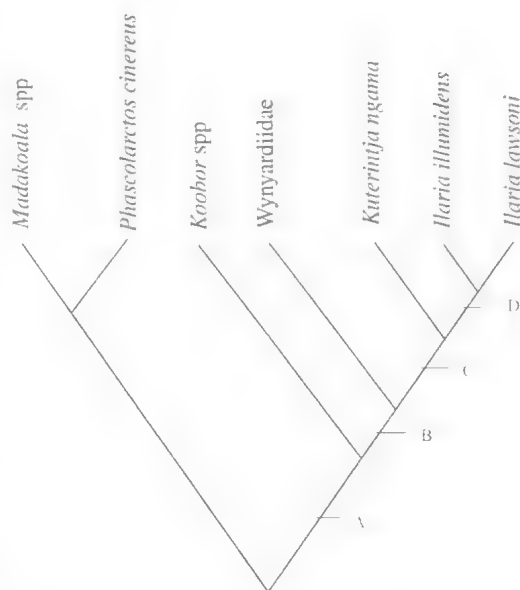


FIG. 6. Relationships of the Ilariidae and *Koobor*. DELTRAN Synapomorphies: A-weak longitudinal valley; B-well-developed styler cuspids; moderately developed transverse valley; separation of styler cuspids C and D; weak paraconule on M^1 ; no protostylid; protoconid > metaconid; no compression of lingual portion of tooth; moderate crown height; dorsally flattened and distally inflected I_1 ; no longitudinal valley; C- well-developed transverse valley; poorly developed postprotocrista and premetaconulecrista; protocone longitudinally compressed relative to metaconule on M^1 - M^3 ; large crown; moderately developed posterolingual cusp on P^3 ; 'central' cuspid; posterolingual cuspid on P_3 ; lingual closure of transverse valley on uppers by a cingulum; non-bladed P_3 and P^3 ; D-moderately well developed transverse linkages; weak paraconid on M_1 ; large teeth; caniniform and conical I_1 . ACCTRAN Synapomorphies: A-moderately developed transverse valley; moderately developed transverse linkages; no protostylid; protoconid > metaconid; dorsally flattened and inflected I_1 ; no posterobuccal cuspid on P_3 ; moderately developed longitudinal valley; B-well-developed styler cuspids; separation of styler cuspids C and D; no paraconule; uncompressed lingual portion of tooth; moderate crown height; moderately developed posterolingual cusp on P^3 ; no longitudinal valley; C-well-developed transverse valley; poorly developed postprotocrista and premetaconulecrista; protocone longitudinally compressed relative to metaconule on M^1 - M^3 ; metaconid a linguallly convex crest; high crowns; 'central' cuspid; posterolingual cuspid on P_3 ; transverse valley closed linguallly by cingulum; non-bladed P_3 and P^3 ; bulbous P^3 ; D-poorly developed paraconule; weak paraconid on M_1 ; large teeth; caniniform, conical I_1 ; posterobuccal cuspid on P_3 ; and P^3 .

cage. Poorly-developed transverse linkages in *Ku. ngama* would therefore be the result of a reversal to the phascolarctid state. The ACCTRAN model appears preferable, although discovery of a lower dentition for *Koobor* would help resolve its classification.

The poorly-developed paraconule on M^1 of *Ilaria illumidens* (Tedford & Woodburne, 1987), is either a plesiomorphy dating from some time after divergence of *Koobor* (DELTRAN), or the result of a reversal (ACCTRAN). The former hypothesis implies that loss of the paraconule is convergent between wynyardiids and *Ku. ngama*, while the latter, and possibly more parsimonious, hypothesis suggests that the paraconule was already lost from the vombatomorphian lineage before the wynyardiids and ilariids diverged.

The paraconid on M^1 is another homoplastic character. For both algorithms character transformation suggests that a well-developed paraconid is convergent between *I. illumidens* and *Madakoala*. A poorly developed paraconid is deemed to be convergent between species of *Ilaria* and primitive *Madakoala*, with absence of a paraconid being the plesiomorphic phascolarctid character state. However, a more likely solution is: 1) that a well-developed paraconid is the plesiomorphic condition; 2) that absence of a well-developed paraconid in *P. cinereus* is a derived condition; 3) that the paraconid was gradually reduced or lost before or after *Koobor* diverged; 4) that the paraconid in species of *Ilaria* represents a reversal to the plesiomorphic state; and 5) that loss of a paraconid is convergent between *P. cinereus*, wynyardiids and possibly *Koobor*. Knowing whether there was or was not a paraconid in *Koobor* would help clarify this situation.

Both algorithms suggest that a protostylid on M^1 of *Ilaria illumidens* represents a reversal to the plesiomorphic phascolarctid condition. The only discrepancy between the two character transformation pathways is the point at which the protostylid was lost. DELTRAN delays loss of the protostylid until after the divergence of *Koobor*, while ACCTRAN maintains that loss occurred before the divergence. An identical character transformation occurs for 'relative heights of the anterior cuspids' (character 11), such that cuspids which are subequal in height represent a reversal to the plesiomorphic condition for *I. illumidens*. Possessing a protoconid larger than the metaconid is therefore a synapomorphy uniting wynyardiids, *I. lawsoni*, *Kuterintja ngama* and possibly *Koobor*. A

posterobuccal cuspid on P^3 of species of *Ilaria* is deemed to be a reversal to the plesiomorphic phascolarctid condition by ACCTRAN, while DELTRAN suggests that absence of this structure is convergent between wynyardiids and *Kuterintja ngama*. Again, ACCTRAN seems to be the most parsimonious, implying that the posterobuccal cuspid was lost before wynyardiids and ilariids, and possibly *Koobor*, diverged.

For lingual closure of the transverse valley on upper molars (character 20) the pathway for character transformation is unclear due primarily to the variable nature of this structure in *Madakoala*. However, the suggested transformation sequence is: 1) a partial cingulum, in the form of 2 cuspules on the anterolingual and posterolingual bases of the metaconule and protocone respectively, was present in the ancestral koala; 2) the two cuspules eventually joined, convergently forming the derived lingual cingulum in *P. cinereus*, some specimens of *Madakoala* and ilariids; and 3) other *Madakoala* and wynyardiids developed in the opposite direction, convergently losing the cuspules altogether. The two cuspules occur in *Koobor notabilis* but not in *Koobor jimbarati* (Archer, 1977), perhaps suggesting that the latter is more derived than the former. Alternatively, a lingual cingulum may be a plesiomorphic phascolarctid condition, implying that the cuspules in *Ko. notabilis* are an apomorphic vestige. In this case, absence of a lingual cingulum would be a more derived condition, convergent between some specimens of *Madakoala*, *Ku. jimbarati* and wynyardiids.

The final character transformation found to contain some degree of homoplasy involved a cusp on the posterobuccal margin of P^3 (character 23). The sequence of change suggested by the algorithms is that absence of such a cusp is the plesiomorphic condition, and that species of *Madakoala*, *Ilaria illumidens* and possibly *I. lawsoni* convergently share a derived posterobuccal cusp. This transformation sequence seems unlikely because *Madakoala* are overall more plesiomorphic phascolarctids (Woodburne et al., 1987) and a posterobuccal cusp on P^3 is more likely to be the plesiomorphic condition. If so, loss of this structure is a synapomorphy for *Koobor*, wynyardiids and *Ku. ngama*, and is convergent on the condition in *Phascolarctos cinereus*. Absence of the cusp in this context is yet another potential character state separating *Koobor* from phascolarctids.

According to Simmons (1993) the expected

value for the consistency index of a tree with 7 taxa is:

$$CI = 0.90 - 0.022 (7) + 0.000213 (7)^2 = 0.736 (3 \text{ s.f.})$$

The observed CI for the optimal intrafamilial tree is 0.800, 0.064 from the expected value. The observed CI value implies slightly less homoplasy for the intrafamilial analysis than would be expected for seven taxa. Similarly the retention index (RI) and the rescaled consistency index (RC) are reasonably large, emphasising the low degree of homoplasy and potential for homoplasy respectively.

The optimal tree which includes all outgroup taxa is reasonably well-supported by bootstrap analysis and by the lack of significantly different trees, of plausible topology, within a few steps of the most parsimonious. The low bootstrap result for the *Ilaria* clade is almost totally due to the amount of missing data for *I. lawsoni*. This study supports the notion that *Ku. ngama* is an ilariid and forms a monophyletic clade with *Ilaria*.

CLASSIFICATION OF *KOOBOR*

Pledge (1987) discussed the possibility that *Kuterintja ngama* is more closely related to *Koobor* than *Ilaria*. The lower dentition and upper molars in addition to M³ demonstrates that *Ku. ngama* is an ilariid. One of the few similarities between *Koobor* and *Kungama* is the smooth rounding of the lingual faces of the lingual cusps, a character state previously thought to unite the taxa phyletically (Pledge, 1987). However, smooth and rounded lingual faces on lingual cusps are also a feature of wynyardiids, and to a lesser extent *Madakoala*, suggesting that it is plesiomorphic. The ambiguity of this character state also increases the possibility of homoplasy. Pledge (1987) hypothesised that *Ku. ngama* may be ancestral to *Koobor*. Our study does not support this view.

Koobor notabilis appears to be the primitive sister-group of wynyardiids plus ilariids. We have no clear support, however, for *Koobor* being in the Phascolarctidae. This may be indirect support for the suggestion that *Koobor* represents a distinct family of vombatiform marsupials. DELTRAN found only one synapomorphy potentially uniting *Koobor* with the wynyardiids and ilariids: the less well-developed longitudinal valley on the molars. ACCTRAN found 7 synapomorphies for a *Koobor*, wynyardiid and ilariid clade. This should not be taken at face value, however, as 6 of these character states refer to the lower dentition which is unknown for *Koobor*. 10

synapomorphies were found by DELTRAN to unite wynyardiids and ilariids to the exclusion of *Koobor* (Fig. 6).

BIOCORRELATION OF RIVERSLEIGH AND THE ETADUNNA FORMATION

Ku. ngama occurs in the White Hunter Local Fauna at Riversleigh and in the Ngama Local Fauna in the upper Etadunna Formation. *Ilaria lawsoni* occurs in the Ditjimanka Local Fauna in the lower Etadunna Formation. *Ilaria illumidens* occurs in the Pinpa Local Fauna of the Namba Formation, at Lake Pinpa.

Woodburne et al. (1993) suggested at least 6 magnetic reversals within the Etadunna sequences, correlated them with a biostratigraphic zonation and the MPTS (Fig. 7) and suggested 24–28 Ma for the base of the Etadunna Formation.

Woodburne et al. (1993) correlated Zone D with the Ngama and Tarkarooloo Local Faunas. Correlation of magnetic polarity and biostratigraphic zones places zone D in lower magnetozone R3, which in turn correlates with Chron 7n.1r of the MPTS, or 24.7–25.0 Ma. *Ku. ngama* therefore, correlates White Hunter Site with the Ngama Local Fauna at 24.7–25.0 Ma providing: 1) that ilariid material in White Hunter Site has not been reworked from older deposits (which, given the lack of evidence for weathering or transport, does not appear likely); and 2) that the apparently short temporal range of *Ku. ngama* in the Etadunna Formation is the full range of this species.

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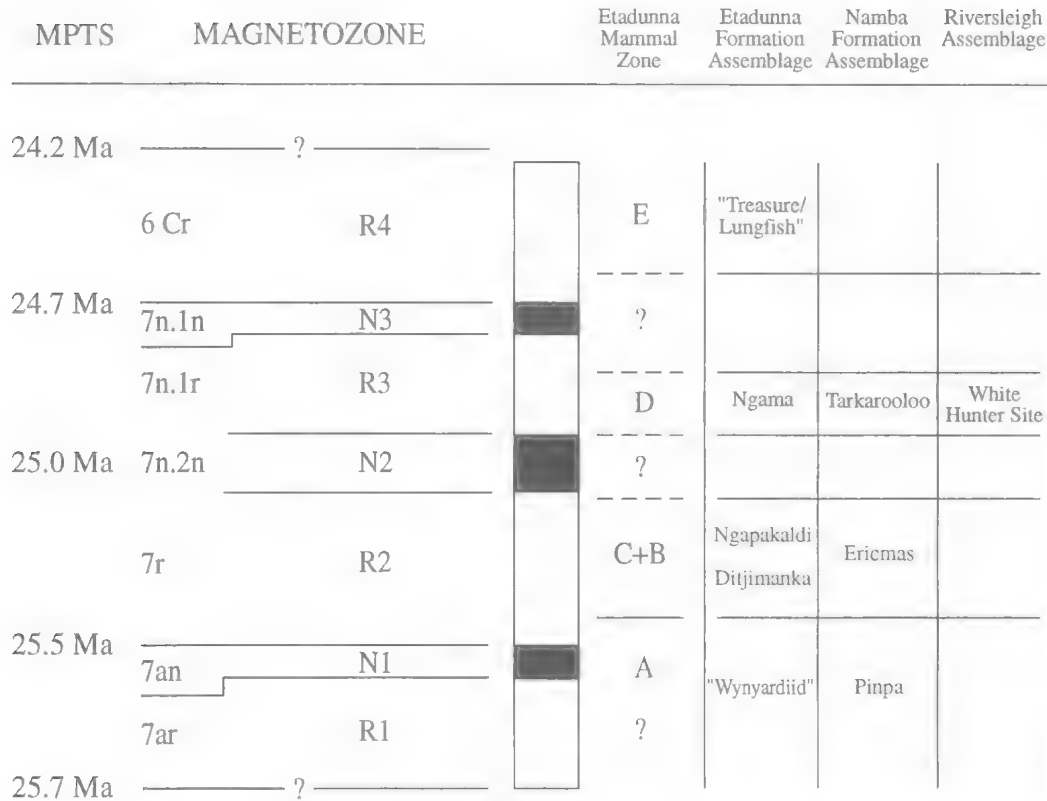


FIG. 7. Geochronology and biocorrelation of the Etadunna and Namba Formations, Lake Palankarina and Lake Pinpa, S.A. and lower Riversleigh faunas, northwestern Queensland. (Modified from Woodburne et al., 1993, figs 2 and 15). N = Normal magnetic polarity; R = Reversed magnetic polarity; MPTS = magnetic polarity time scale.

from many hundreds of volunteers as well as staff and postgraduate students of the University of New South Wales. Skilled preparation of most of the Riversleigh material has been carried out by Anna Gillespie. TJM acknowledges the assistance of Prof. Alberto Albani, Karen Black, Jenni Brammall, Henk Godthelp, Steve Salisbury, Anne Musser, Mary Knowles and his family.

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**NANOWANA GEN. NOV., SMALL MADTSOIID SNAKES
FROM THE MIOCENE OF RIVERSLEIGH: SYMPATRIC SPECIES
WITH DIVERGENTLY SPECIALISED DENTITION**

JOHN D. SCANLON

Scanlon, J.D. 1997 06 30: *Nanowana* gen. nov., small madtsioid snakes from the Miocene of Riversleigh: sympatric species with divergently specialised dentition. *Memoirs of the Queensland Museum* 41(2): 393-412. Brisbane. ISSN 0079-8835.

Two small early Miocene madtsioid snakes from Riversleigh, NW Queensland are described as *Nanowana godthelpi* gen. et sp. nov. and *N. schrenki* gen. et sp. nov. Jaw elements of the former are depressed, lack ankylosed teeth, and have alveoli of nearly uniform size; these features are interpreted as signs of a coadapted character complex ('arthrodonty') where the teeth are attached to the jaws by a fibrous hinge. This condition is associated with a diet of hard-scaled scincid lizards. The latter species retains ankylosis, and has strongly enlarged teeth on the anterior dentary and middle maxilla indicating a distinct method of subduing prey, but extant analogues are also predominantly scincivorous. Departure in each species from the nearly homodont, ankylosed condition in other madtsioids is interpreted as adaptation to a diet of scincid lizards. These divergent, but functionally parallel specialisations are likely to be independently derived from the ancestral condition.

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Madtsioid snakes in Tertiary faunal assemblages of Riversleigh (Scanlon 1992, 1993, 1995, 1996) have been referred to *Yurlunggur* Scanlon, 1992 and *Wonambi* Smith, 1976. Other Riversleigh madtsioids cannot be included in previously known genera. Two small species, estimated to reach 1 m long, are represented by upper and lower jaw elements from System B (Archer et al., 1989, 1994) on Godthelp Hill. Some are associated with vertebrae, but the two species cannot be distinguished unambiguously on vertebral characters. I include them in a single genus which possibly unnatural treatment allows generic identification of isolated vertebrae from other sites.

This paper provides descriptions of the two species including some ontogenetic stages. While analysis of phylogeny of madtsioids awaits detailed comparisons with other primitive snakes, some functional and evolutionary points are noted by analogy with extant forms.

MATERIALS AND METHODS

Material is housed in the Queensland Museum (QMF), Australian Museum (AMF), Northern Territory Museum of Arts and Sciences (NTMP), Museum of Victoria (NMVP), and South Australian Museum (SAMP). ... (SMNR) specimens examined in Paris by courtesy of J.-C. Rage.

Teeth or alveoli are numbered beginning from the anterior on complete jaw elements; on fragments where the tooth row is or may be incom-

plete anteriorly the numbers are spelled out in words. In illustrating cranial bones, views of the same specimen are usually arranged parallel to each other, in lateral, dorsal, medial, ventral aspects. Figures of vertebrae have left lateral, anterior, posterior, dorsal, and ventral views of each element in a vertical row. If more than one vertebra are shown in an illustration, they are arranged (l to r) in order from anterior to posterior.

SYSTEMATICS

Family MADTSOIIDAE Hoffstetter, 1961

Nanowana gen. nov.

TYPE SPECIES. *Nanowana godthelpi* sp. nov.

OTHER SPECIES. *Nanowana schrenki* sp. nov.

ETYMOLOGY. Greek *nanos*, a dwarf and Warlhirri (Tanami Desert, central NT) *Wana*, Rainbow Serpent of Aboriginal mythology.

DIAGNOSIS. Small, upto 1.5 m long; neural spine low to moderately high, not extending close to anterior edge of zygosphene; zygosphene shallow, with anterodorsal edge straight, slightly convex or concave in dorsal view; subcentral ridges well-defined, straight or slightly concave or convex in ventral view; haemal keel relatively narrow, with 'paired hypapophyses' in posterior trunk defined laterally, but not projecting ven-

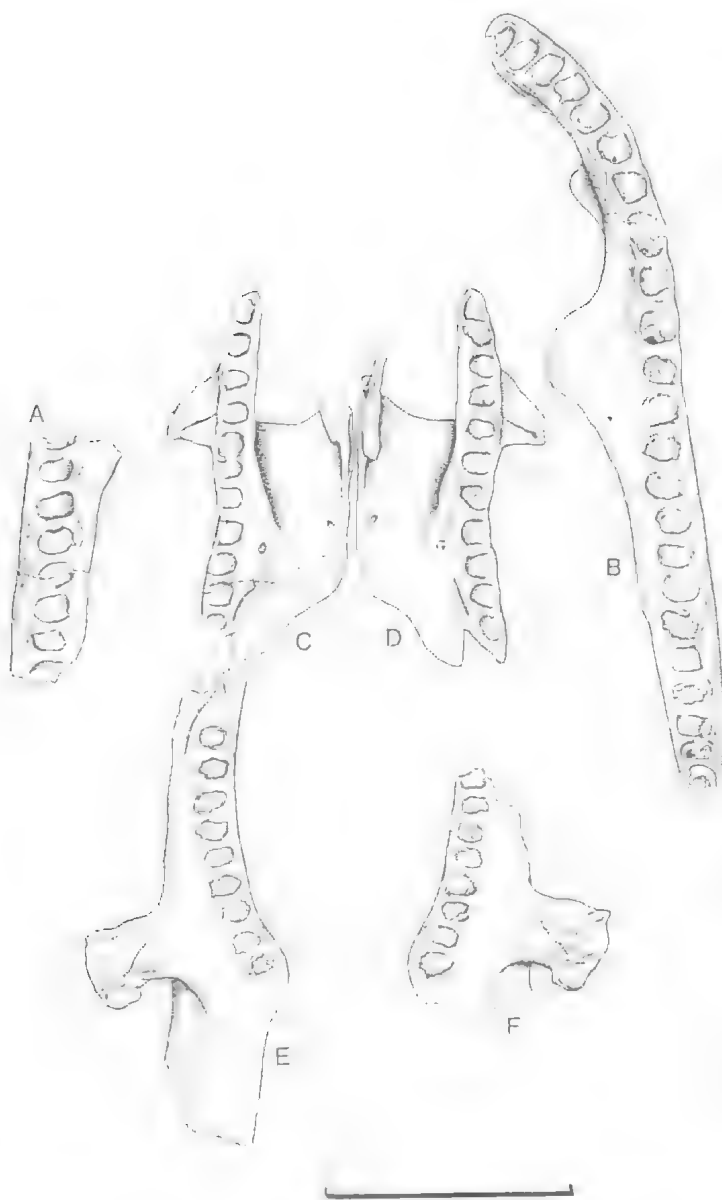


FIG. 1. *Nanowana godthelpi* sp. nov., QMF31379, holotype, upper jaw bones (right (A) and left (B) maxillae, palatines (C, D) and pterygoids (E, F) of a single individual) in palatal view, CS Site. Scale bar=5mm.

trally or separated by a median concavity; neural arch in posterior trunk depressed, its lateral portions strongly concave dorsad. Anterior tip of maxilla with medial expansion (septomaxillary process) contributing to floor of narial chamber;

dorsal process with steep anterior edge; dentary with at least 2 mental foramina.

COMPARISON. This genus is distinguished from all madtsoiids other than *Alamitophis* by the zygosphene in dorsal view frequently (but not always) having a convex anterior margin; the convexity is broad rather than a distinct median tubercle as in *Alamitophis*. It is distinguished from *Yurlunggur*, *Wonambi*, *Rionegrophis*, *Gigantophis* and *Madtsoia* by being smaller. Its neural spines are lower, at corresponding positions in the trunk, than in *Madtsoia*, *Rionegrophis*, *Wonambi* and *Alamitophis*, but higher than *Patagoniophis* or *Gigantophis*. It is distinguished from all genera except *Patagoniophis* by the less steeply converging subcentral ridges (relatively more elongate centrum in ventral view). Maxillae resemble *Madtsoia* sp. (SMNR 2879, Itaborai) and are distinguished from *Wonambi* and *Yurlunggur* by prefrontal process having a steep anterior edge; distinguished from each of these by development of the septomaxillary process (condition unknown in other madtsoiids).

DISCUSSION. Vertebrae can be distinguished from other madtsoiids, but their common features (including small size) may be symplesiomorphic; the concept of *Nanowana* containing these 2 species can be described as a 'marriage of convenience'. The phylogenetic relationships of these with other madtsoiids remain unknown, but they are treated as a unit because their vertebrae (which provide

the only taxonomically useful material in most deposits) are unable to be distinguished in many cases.

In a number of aspects of the vertebrae, including size, *Nanowana* is comparable to *Patagoniophis* sp. cf. *P. parvus* from the early Eocene Tingamarra Local Fauna (Scanlon 1993); differences include the higher neural spine (in adults), narrower haemal keel in the posterior trunk, frequently convex anterior edge of the zygosphenes, and dorsolateral concavities of the posterior neural arch. It differs from *Alamitophis*, which also occurs in the Australian Eocene (Scanlon, 1993): the anterior edge of the zygosphenes, when convex, is broadly so rather than forming a distinct prominence; paradiapophyses do not project anteriorly; zygapophyses are more steeply inclined at equivalent positions within the column. The lower neural spine, broader zygosphenes, and features of the haemal keel or hypapophyses differentiate *Nanowana* from *Wonambi* Smith, (1976) (*Wonambi* is known from Riversleigh, much smaller than *W. naracoortensis* but larger than *Nanowana*; Scanlon, 1996).

The only other known Australian madtsoiid is *Yurlunggur*, at least 2 species of which occur at Riversleigh as well as the type species from Bullock Creek (middle Miocene; Scanlon 1992). That genus exceeded 5m and thus included only 'giant' snakes, though not as large as *Gigantophis garstani* or *Madisoia bai*. However, size is rather variable in many snake genera (e.g. the pythonid *Morelia*, sensu Underwood & Stimson, 1990, includes species with maximum

lengths from under 1m to over 7m), and need not be considered an essential part of the diagnosis. The vertebrae of small and large forms are rather similar except in features which may be directly related to size (neural spine height is variable

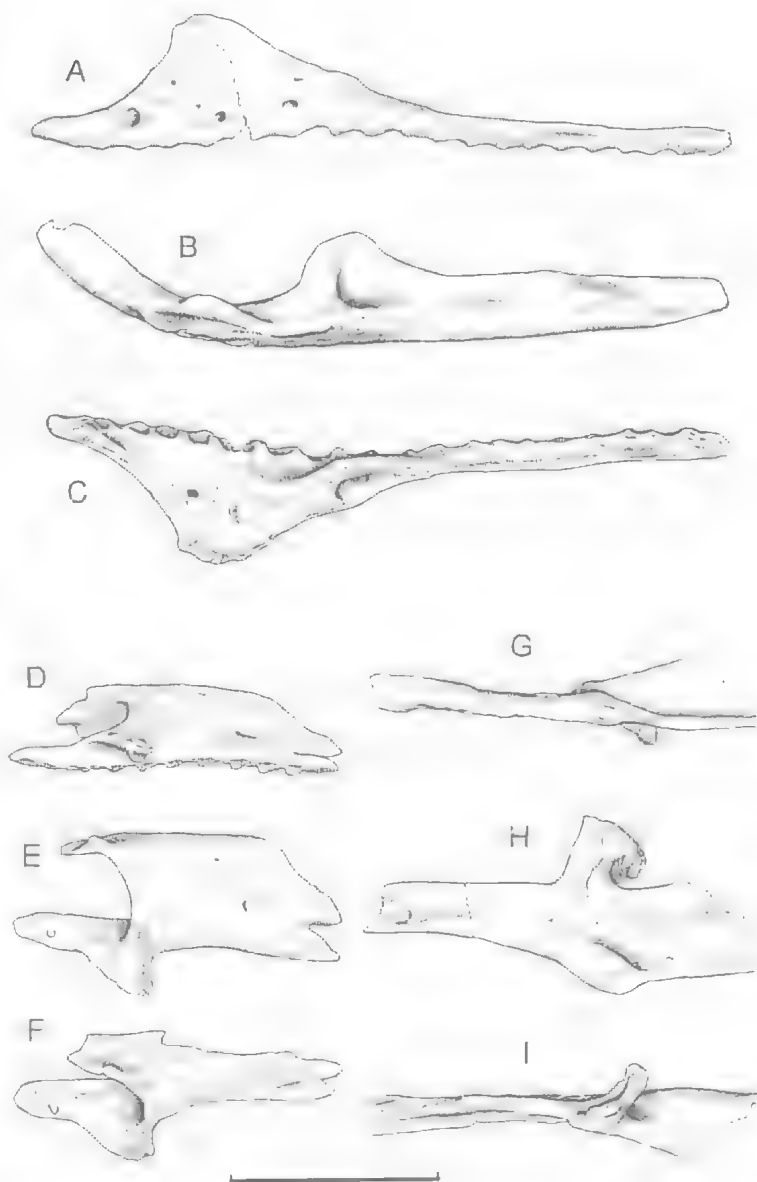


FIG. 2. *Nanowana godthelpi* sp. nov. QMF31379, holotype, upper jaw bones (left maxilla (A-C), left palatine (D-F) and right pterygoid (G-I)) in lateral, dorsal and medial views, CS Site. Scale=5mm.

within *Yurlunggur*, and is proportionally similar to *Nanowana* in some), but *Nanowana* differs from *Yurlunggur* in the shape of the zygosphenes, and the haemal keel of posterior trunk vertebrae being narrower and lacking a median concavity.

Comparisons with non-Australian forms do not suggest any links closer than that with *Yurlunggur*, and will not be pursued here. The rib-heads of *Nanowana* have not been considered in detail, but appear to be similar in shape to those of *Yurlunggur* and *Wonambi* (Scanlon, 1993).

***Nanowana godthelpi* sp. nov.**
(Figs 1-8, Table 1)

ETYMOLOGY. For Henk Godthelp, University of New South Wales, in recognition of his contributions to Australian palaeontology.

MATERIAL. Holotype QMF31379, associated elements of a single individual comprising partial to complete maxillae, palatines and pterygoids of both sides. Paratypes QMF31383, 31384 associated dentaries and compounds of a single individual; dentaries QMF20892, 23052, 23053, 23054, 23056; maxillae QMF31380, 31382, 31386, 31387; palatine QMF31381; pterygoids QMF23058, 31393. All types from early Miocene (System B) Camel Sputum Site, Godthelp Hill. Other material: Camel Sputum Site, trunk vertebrae QMF19741. Upper Site, dentary QMF31389; palatine QMF23066; maxilla fragment QMF31390; pterygoids QMF23067, 31385; series of cloacal vertebrae. Mike's Menagerie Site, anterior fragment of pterygoid QMF19742. Creaser's Ramparts Site, dentary QMF23076.

DIAGNOSIS. Palatine lateral process about as long as two alveoli (nearest to 4th and 5th), ventral concavity of process with obtuse angle accommodating posterolateral angle of palatine process of maxilla. Maxilla with 23 tooth positions, palatine 11, pterygoid 9, dentary 16. Teeth not ankylosed to alveoli; maxillary alveoli vary only slightly in size, dentary alveoli largest in centre of tooth row (4-8 or 5-8). Posterior part of maxilla strongly depressed. Dentary tooth row curved in dorsal view. Two or 3 mental foramina, all anterior to the 7th alveolus.

DESCRIPTION OF HOLOTYPE. Upper dentigerous elements in a single block (without vertebrae or other elements) are complete on one or both sides, missing bilaterally only the posterior (quadrate) processes of the pterygoids (Figs 1,2). Maxillae long and flat posteriorly, supporting a high lizard-like prefrontal process anteriorly; palatines with 'alethinophidian' features; pterygoids

with prominent, also lizard-like, ectopterygoid processes. Proportions of jaws indicating a relatively long postorbital skull and moderately short, rounded snout.

Palatine: Left more complete than right, both well-preserved. Eleven alveoli forming a sigmoid tooth row, convex laterad anterior to an inflection and lateral concavity (slight, but definite and angular) between 7th and 8th. Dorsolateral crest arising above 3rd alveolus, bifurcating above 4th to form anterior edges of maxillary and choanal processes. Maxillary process with an oblique anterior edge (near 45° from sagittal plane), longitudinal lateral edge and transverse posterior crest on its ventral face, level with the 5th alveolus on the left palatine (4th-5th on right side); process not perforated or notched for the maxillary nerve. Anterior edge of the choanal process smoothly concave anteriorly for its full width, reaching between level of 4th and 5th alveoli; then curving strongly anteroventrally, extending to front of 2nd alveolus. Vertical anteromedial part of the choanal process bilobed anteriorly, a dorsal lobe curved medially, the other laterad (forming articulations with the parasphenoid and vomer); third, posterolaterally pointed, lobe on the ventral edge deflected laterad, contributing (along with the vomer and ectochoanal cartilage, presumably) to the floor of the choanal passage. Lamina of choanal process strongly arched anteriorly, flatter posteriorly, and ventrally deflected part of lamina reducing in depth posteriorly. Posteromedial corner of process level with rear of 9th alveolus, posterior margin sinuous so that posterior process not sharply demarcated (as in some specimens); margin concave medially, convex posteriorly. Posterior extremities of choanal process and tooth row extending back level with each other, both with lateral margin parallel to tooth row, and separated by a distinct triangular notch extending forward to middle of 11th alveolus (thus, posterior edge W-shaped); on dorsal face this notch continued as a tapering trough extending to rear of 9th; ventrally a step-like groove running from the apex of the notch anteromedially to between 9th and 10th, with a shallow trough posterior and partly medial to the groove. Small foramen dorsomedially on the dentigerous process, just below the ridge continuous with the anterior edge of the choanal plate; a large foramen medial to the 8th alveolus, piercing the plate and emerging dorsally as a posteriorly widening foramen between 8th and 9th; another small foramen anteromedial to 10th alveolus. Dorsomedially on the anterior dentigerous process with tip of a tooth

emerging from the bone (this is the only tooth associated with jaws of this species).

Right and left palatines almost identical; spacing of alveoli slightly different on different sides; alveoli 2-5 in the right shifted posteriorly, relative to the left (alveoli 1 and 2 on the left, 5 and 6 on the right, confluent). Lateral (maxillary) process with small but distinct angular concavity marking the longitudinal (lateral) and oblique (anterolateral) sections of the margin.

Pterygoid. Nine alveoli (complete row), anterior tip (length of approximately 1.5 alveoli) edentulous. Tooth row curving medially posteriorly, following inner edge of bone; ventral face narrowing to a point anterior to tooth row, point interlocking with posterior notch of palatine. Dorsal surface forming a longitudinal trough, with foramen above 1st alveolus (opening anteriorly), lateral to a dorsomedial ridge. Lateral margin smoothly convex, diverging gradually from tooth row; anterior edge of ectopterygoid process diverging at about 120° from this margin, level with 7th alveolus. Process nearly as wide as rest of bone at this point, about as long as wide; its anterior and lateral edges at 90° in dorsal or ventral view, lateral margin inclined strongly posteroventrally, with posterior extremity produced as a knob-like extension, and posterior edge strongly concave. No part of the ectopterygoid facet exposed dorsally. Concave posterior surface of the process continuous with the ventrolateral face of the posterior lamina (quadrate process), bounded

medially by a narrow extension of the ventral (occlusal) surface. Quadrate process broken off

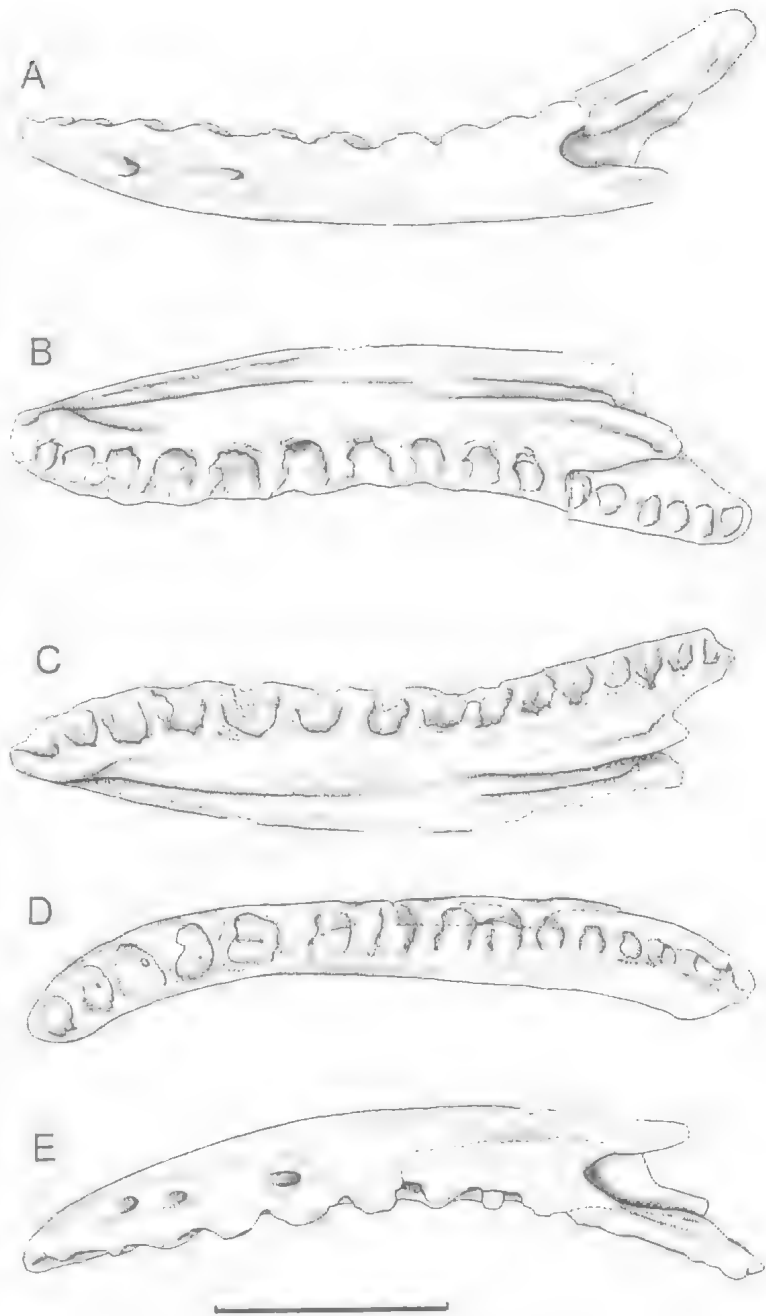


FIG. 3. *Nanowana godthelpi* sp. nov. QMF31383, 31384, paratype lower jaws. A, B, left dentary in lateral and medial view (upper posterior process broken and slightly displaced). C, D, E, right dentary in medial, dorsal, and lateral view. Scale=5mm.

TABLE 1. Measurements (mm) of jaws of *Namowana godthelpi* sp. nov. C1, C2, etc.=single individuals; L=left, R=right. Alveoli were selected as landmarks for some measurements because they could be identified in fragments, but there is variation in the position of anterior alveoli (even between sides of an individual). Values in brackets are minima for measurements affected by damage.

Palatine (ventral view): ptl=length of palatine from anterior tip of dentigerous process to posterior tip of tooth row spine or choanal process; pcl=base length of choanal process from intersection of anterior edge with dentigerous process to apex of posterior notch; pl11=length from anterior tip to anterior edge of 11th alveolus; ptw=width across choanal and maxillary processes; pcw=width in same line of choanal process; prw=width in same line of tooth row bar; pmw=width in same line of maxillary process.

Pterygoid (ventral view): ttl=length from anterior spine (in plane of alveoli, not dorsal lappets) to rear of 9th alveolus; trl=tooth row 1st-9th alveolus; tte=from anterior spine to furthest point of ectopterygoid process; tl5=length across most posterior 5 alveoli (5-9); taw=width between near-parallel edges anterior to ectopterygoid process; tpw=width from basipterygoid facet to intersection of ectopterygoid process and dorsolateral edge of posterior lamina; ttw=width from basipterygoid facet to furthest point of ectopterygoid process.

Maxilla: mtl=length; map=length from anterior tip to posteromedial angle of palatine process; m712=length from anterior edge of 7th-13th alveolus; mpw=width across palatine process; mph=depth at prefrontal process.

Dentary: mff=number of mental foramina; dtl=straight-line length; dl15=length to anterior tip of 15th alveolus; dl5=length to lateral fossa; d4t= posterior edge of 4th alveolus to posterior extremity; d415=posterior edge of 4th to anterior edge of 15th; d4f= posterior edge of 4th to lateral fossa; dl7=anterior tip to anterior edge of 7th alveolus; dmd=depth from dorsolateral to ventromedial edge in middle part of bone; dpp=depth of upper posterior process.

QMF	31379		31381	23058	31386	31380	31382	31393	23066	23067	31385
Ind.	C1 R	C1 L	C2 L	C2 L	C2 R	C3 R	C3 L	C4 R	U1 L	U1 R	U1 L
ptl	(7.6)	7.7	(8.0)	-	-	-	-	-	-	-	-
pcl	4.4	4.2	4.0	-	-	-	-	-	4.5	-	-
pl11	6.6	6.7	6.8	-	-	-	-	-	-	-	-
ptw	3.9	(3.8)	4.0	-	-	-	-	-	3.8	-	-
pcw	1.9	1.9	2.0	-	-	-	-	-	2.0	-	-
prw	0.9	0.9	1.1	-	-	-	-	-	1.0	-	-
pmw	1.1	(1.0)	(0.9)	-	-	-	-	-	(0.8)	-	-
ttl	5.7	-	-	-	-	-	-	-	-	-	-
trl	4.9	-	-	-	-	-	-	-	-	-	-
tte	6.8	-	-	-	-	-	-	-	-	-	-
tl5	2.6	2.5	-	3.2	-	-	-	1.6	-	3.1	3.0
taw	1.7	1.6	-	1.7	-	-	-	(1.0)	-	1.6	1.6
tpw	2.4	2.4	-	3.1	-	-	-	-	-	2.9	3.0
ttw	4.2	4.1	-	(3.9)	-	-	-	-	-	4.3	(3.9)
mtl	-	(16.3)	-	-	-	-	-	-	-	-	-
map	-	7.4	-	-	-	-	-	-	-	-	-
m712	-	5.4	-	-	5.7	4.6	5.2	-	-	-	-
mpw	-	2.3	-	-	(2.8)	2.8	2.8	-	-	-	-
mph	-	(3.3)	-	-	3.9	3.6	3.3	-	-	-	-
Dentaries											
QMF	31383	31384	20892	23052	23053	23054	23056	31389	23076		
Ind.	C1 R	C1 L	C2 L	C2 R	C3 L	C3 R	C4 R	U1 L	C1 L		
mff	3	2	2	3	2	-	2	3	-		
dtl	-	-	-	15.1	-	-	-	-	-		
dl15	15.6	-	14.1	13.3	-	-	-	-	-		
dlf	12.3	-	11.4	11.2	-	-	-	12.4	-		
d4t	-	13.6	-	11.9	-	-	-	-	16.3		
d415	11.3	12.3	11.1	10.2	-	-	-	-	14.2		
d4f	8.0	9.5	8.2	8.2	-	7.7	4.9	9.6	11.0		
dl7	7.8	-	6.5	6.3	8.0	-	-	-	-		
dmd	3.2	3.0	2.7	2.6	3.3	(2.4)	1.6	2.9	(2.6)		
dpp	1.0	0.9	0.9	0.9	-	-	-	-	1.4		

posteriorly about half the length of the tooth row behind the ectopterygoid process. Basipterygoid articular surface opposite ectopterygoid process, an oval facet facing dorsally and slightly medially, beginning level with front of 8th alveolus and extending to beyond 9th, only slightly distinct in outline from the rest of the medial edge. Apart from the anterior foramen mentioned above, 3 foramina dorsally, anterior, lateral and posterior to the facet; anterior 2 near the midline of the bone, posterior foramen close to the medial edge. A shallow but distinct transverse groove on the dorsal surface of the ectopterygoid process.

Left pterygoid retaining posterior 8 alveoli, which are slightly smaller and more closely spaced than on the right; possibly a 10th alveolus or longer edentulous gap anteriorly.

Maxilla. Alveoli 23, varying only slightly in size; row curved medially anteriorly, straight posteriorly. Anterior alveoli elongate anterolateral-posteromedially; anterior of maxilla wider than deep, with dorsomedial edge forming a crest above 1st-3rd alveoli, with slight concavities dorsal and medial to it. In lateral view, ventral margin slightly convex up to 10th alveolus, nearly straight posteriorly; dorsal edge rising smoothly and increasingly steeply from the anterior tip to between 6th and 7th alveoli; highest part of the dorsal process (7th to 9th) forming the dorsomedial surface for articulation with the prefrontal. On the posterior slope of the process, a low prominence above the 11th alveolus probably the insertion site for the postorbital ligament, but may also mark the anterior extent of the jugal; by 13th bone very shallow, continuing so to the posterior extremity. Large lateral (trigeminal) foramen opening anteriorly above the 5th-6th alveoli; two smaller foramina, equally close to ventral edge, above 7th-8th and 9th-10th, and 3 small foramina higher on the prefrontal process. Medial edge forming a shelf-like 'septomaxillary' process from 2nd to 4th alveolus, separated from the palatine process which widens gradually from 7th and then sharply at 10th, then gradually approaches maximum width at a sharply obtuse posteromedial angle between 11th and 12th. Medial shelf narrowing steeply from this point, then very gradually, but with a step-like inflexion at level of 18th alveolus (marking location of anterior tip of ectopterygoid). Large foramen entering maxilla at broadest part of the palatine process, above 11th alveolus, and a smaller foramen exits at the same level above the 7th. Tooth row following lateral margin closely from 1st-11th alveoli, then gradually crossing over with 19th-23rd

closer to medial edge; lateral edge forming a low dorsolateral crest (possibly homologous with more prominent crests or bulges in snakes such as *Dinilysia* and pythons). Lateral as well as medial parts of posterior maxilla apparently overlapped by the ectopterygoid, forming slight concavities on either side of a slight dorsal crest. Between ectopterygoid facet and prefrontal process, the suborbital surface with a shallow longitudinal groove which probably either was, or bounded, a facet for the jugal (an element lost in extant snakes but probably retained in *Dinilysia* and madtsoids, including *Wonambi*; Estes et al., 1970; Scanlon, 1996).

PARATYPES. Right and left mandibles (QMF31383, 31384), each compound and dentary, in loose articulation, lacking the splenial, angular and coronoid of each side (Figs 3, 4).

Right: Tooth row incomplete posteriorly, broken through 15th alveolus; no sign of ankylosed teeth. 4th to 8th largest alveoli, subequal, size reducing posteriorly and anteriorly. In lateral view, dorsal edge convex dorsad from 1st to 5th alveolus, concave dorsad for rest of length. Ventral edge slightly concave anteriorly, remainder convex but somewhat worn. Three mental foramina, below 3rd, 4th and 6th alveoli, opening anterodorsad. Posterior lateral fossa (compound notch) extending to between 10th and 11th. Lateral face smooth but with dorsolateral ridge defined by slight longitudinal concavity through foramina. In dorsal view, tooth row concave medially, slightly more so anteriorly; alveoli round or squarish except first two which are somewhat elongate transversely. 15th alveolus on a narrow process distinguished by an angular concavity from the expanded dorsomedial shelf. The medial ridge forming the upper edge of Meckel's groove overhanging the groove distinctly up to the 8th alveolus; the overhanging edge of the upper facet for the splenial beginning below the 8th but more dorsally, forming with a slightly acute, pointed posteroventral process separated by a right-angle notch (in medial view) from the dorsal shelf. Meckelian groove narrowing anteriad, anterior end slightly expanded, communicating by a foramen with alveolus of 1st tooth. Smooth bulb-like swelling overhanging the groove medial to the 1st and 2nd alveoli.

Left: Two mental foramina, between 3rd and 4th, and 5th and 6th. Posterior lateral fossa extending to between 11th and 12th alveoli.

Right compound. Elongate, shallow, 18.8mm long, 16.8mm from anterior tip to dorsal extrem-

ity of articular facet. Surangular lamina low but concave above, forming low coronoid process posterior to articulation with dentary, about 1/3 of length from anterior tip. Maximum depth of compound less than depth of dentary at articulation (suggesting that the coronoid extended dorsal to compound, forming most of the coronoid process by itself). Ventral edge, and lateral in dorsal view, nearly straight, but posterior end (below articular facet and retroarticular process) deflected slightly ventrad and mediad from main shaft. Articular facet dorsal and medial in position, not extending to lateral face, reaching to middle of medial face, and as far anterior as ventrad from dorsal extremity; facet defined posteriorly by a raised transverse lip, followed by a groove anterior to the sigmoid dorsal edge of the retroarticular process. Slight ventrolateral and deeper ventromedial concavities defining a ventral ridge on the retroarticular process. Shaft of compound nearly cylindrical just anterior to articular facet; a small dorsolateral foramen in this region. Mandibular fossa narrow, beginning posteriorly at level of foramen, curved slightly mediad, and extending to half way between posterior edge of coronoid facet and top of coronoid process.

Fossa partly surrounded by the facet for the coronoid anteriorly; anterior half opening below into mandibular foramen. Surangular lamina curved, overhanging the mandibular fossa for most of its length; reducing in height anterior to coronoid process in two steps, reaching a horizontal or somewhat dorsally concave shelf receiving the posterior part of the dentary; lateral

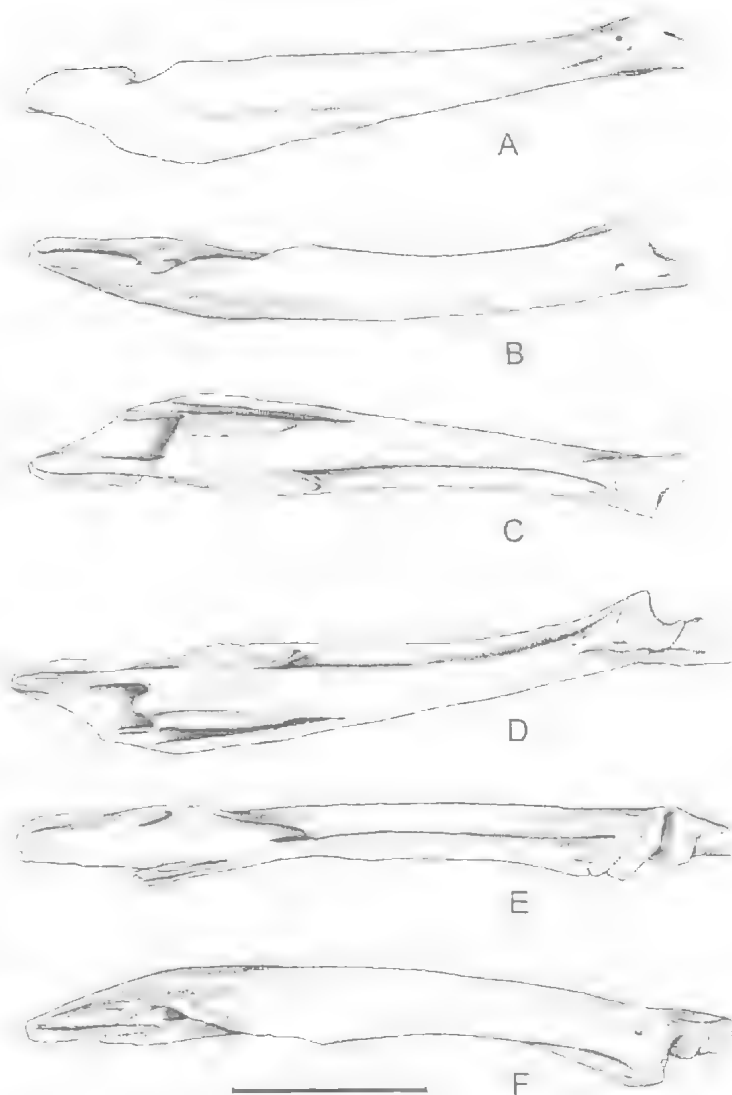


FIG. 4. *Nanowana godthelpi* sp. nov., QMF31383, 31384, paratypes, compound lower jaw bones, CS Site. A-C, left compound in lateral, dorsolateral, and medial views (note missing articular). D-F, right compound in medial, dorsal, and dorsolateral views. Scale=5mm.

edge expanded anterodorsally, for anterior 1/3 of length anterior to the coronoid process. Surangular foramen, opening anteriorly, not exposed laterally or medially, in a shallow dorsal trough between lowest point of surangular lamina and edge of coronoid facet. Facets for coronoid and angular meeting at a very small angle below this point; their line of contact nearly horizontal, only

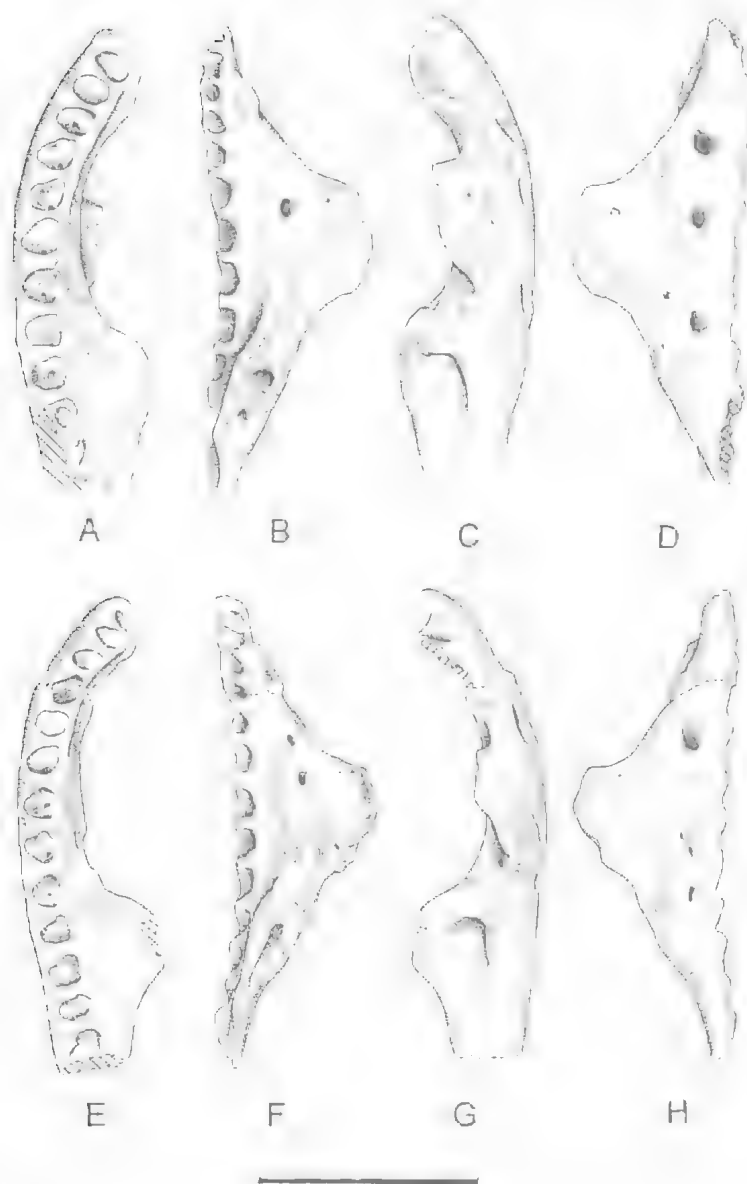


FIG. 5. *Nanowana godthelpi* sp. nov., paratype, maxillae, CS Site, A-D, QMF31386, in ventral, medial, dorsal, and lateral views. E-H, QMF31380, in ventral, medial, dorsal, and lateral views. Scale=5mm.

a short section preserved on either side. In lateral view the anterior edge of the compound rounded dorsally, separated by a right angle from a deeper ventral concavity. In medial view, a long, tapering notch enclosed in the facet for the angular, nearly reaching its posterior end (just posterior to middle of length of compound). A medial anterior process (defined by dorsal and ventral longitudinal fissures) bearing the continuation of facets for the coronoid and angular, and probably also con-

tacting the splenial and dentary, broken on both sides. Left compound similar to the right, but broken posteriorly through the articular facet.

When placed in articulation, the right compound and dentary forming a smoothly curved structure, with total straightline length approximately 29.5mm.

Other paratypes and referred jaw elements (partial dentaries, maxillae, palatines, pterygoids) show some individual variation (Figs 5, 6) and probably ontogenetic changes of proportions (allometry): the smallest dentary, QMF 23056, is relatively deeper than larger specimens (Table 1), while the largest, QMF23076, is relatively slender except for a particularly deep upper posterior process.

Vertebrae. In shape and proportions, vertebrae similar to, and intermediate between *Yurlunggur* and *Patagoniophis* and differ conspicuously from *Alamitophis*, *Wonambi* and *Madtsioia*. Typical anterior, middle and posterior trunk vertebrae recognised (cf. LaDuke, 1991, Scanlon, 1992, 1993); most anterior vertebra possibly 3rd cervical (cf. *Y. camfieldensis* Scanlon, 1992, fig. 1A). Centrum in ventral view relatively long, similar in pro-

portions to *Patagoniophis* sp. but with the sub-central ridges nearly straight rather than strongly concave. Cotyle slightly wider than the zygosphene, which is wider than the neural canal (all about equal in the most anterior vertebra); condyle and cotyle wider than deep, ventral margins flattened in anterior and middle trunk, rounder posteriorly.

Zygapophyseal facets inclined at about 20° from the horizontal (at mid-trunk; flatter anteri-

only, slightly steeper posteriorly), defining planes passing through the internal lateral ridges of the neural canal and intersecting just above its base. Facets broader and more angular in outline (especially the prezygapophyses) in the largest midtrunk vertebrae, with long axes inclined at about 45° from the sagittal plane (somewhat more longitudinal in most anterior and posterior elements). Prezygapophyseal accessory processes lacking, outer face of the prezygapophysis with a buttress-like ridge extending anterolaterally to or slightly beyond the edge of the facet.

Zygosphenes shallower than the neural canal, with facets defining planes intersecting below the floor of the canal; dorsal edge in anterior view flat, slightly arched or arcuate; below it are shallow concavities defining a dorsal ridge and lateral lobes, with sharp ridge separating the anterior face of the zygosphenes from the internal roof of the neural canal. In dorsal view the anteriorly convex dorsal ridge and lateral lobes distinct in mid-trunk vertebrae, but in the most anterior and posterior elements median prominence less developed and zygosphenes broadly concave.

Paradiapophyses similar to *Yurlunggur* or *Patagoniophis*, extending laterally beyond the zygapophyses only in the most anterior and most posterior vertebrae.

Roof of zygantrium horizontal, either uniform in depth or thickening laterally, demarcated from the concave lateral parts of the neural arch by angular 'shoulders', with concavity directed more dorsally than laterally in the most posterior vertebrae because of the shallower neural arch and steeper postzygapophyses.

One or two small paracotylar foramina on either side of the cotyle, usually 2 lateral foramina on either side posterior to the diapophyses. Sub-

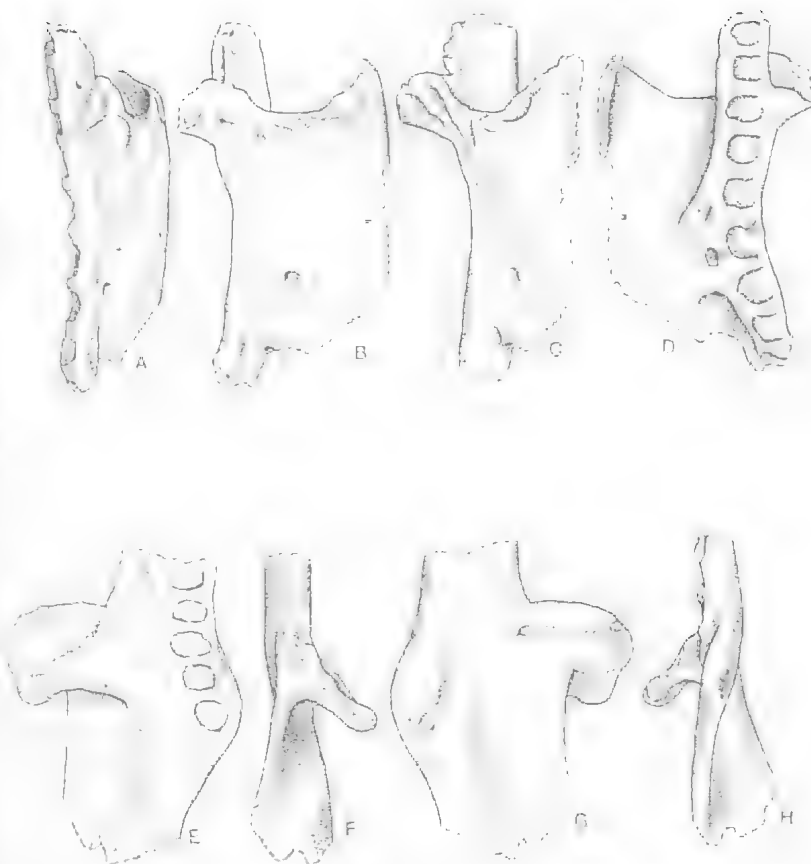


FIG. 6. *Nanowana godthelpi* sp. nov., referred elements from Upper Site possibly from a single individual. A-D, left palatine, QMF23066 in lateral, dorsal, dorsomedial, and ventral views. E-H, right pterygoid, QMF23067, in ventral, lateral, dorsal and medial views. Scale=5mm.

central foramina usually single on each side, small. Parazygantral and zygantral foramina larger, usually single on each side, frequently in distinct fossae. Some vertebrae with small foramina on the anterior face of the prezygapophysis below the facet.

Ventral face of centrum concave between the haemal keel and subcentral ridges. In the anterior trunk hypapophysis projecting well below centrum from its posterior half, with either an angular or sinuous anteroventral edge, and near-vertical posterior edge; in more posterior vertebrae the keel weakly sinuous to nearly straight in lateral profile. Haemal keel with median, keel-like hypapophysis reducing in depth from the cervical to mid-trunk regions; lateral ridges on the keel (initially just posterior to the subcentral foram-

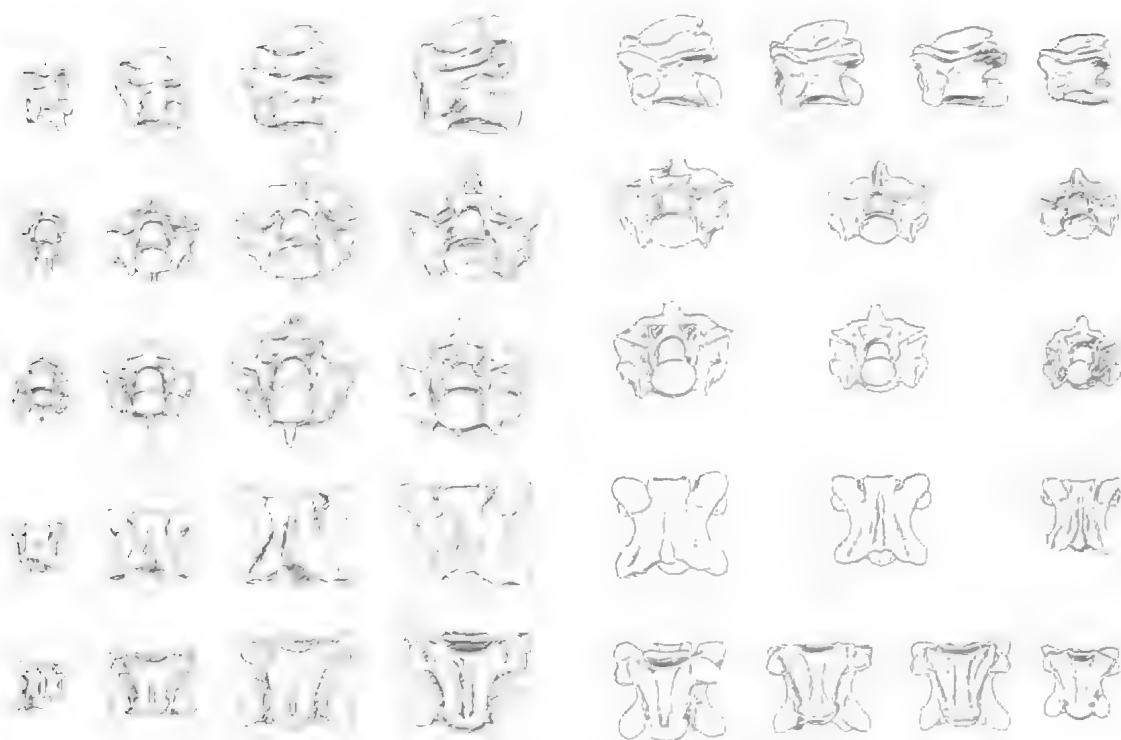


FIG. 7. *Nanowana godthelpi* sp. nov., QMF19741, series of vertebrae from CS Site, possibly from the same individual as the holotype (QMF31379).

ina) from the approximate location of the largest vertebrae in the skeleton, ridges increasing in size in more posterior vertebrae and posterior point of the median keel fading away, leaving the ridges as paired hypapophyses, ventrolateral swellings of the keel. Haemal keel defined by smooth depressions in the anterior trunk, these becoming better defined more posteriorly and approaching the cotylar rim. More posterior vertebrae with distinct channels between keel and subcentral ridges (subcentral paramedian lymphatic fossae, LaDuke, 1991).

Most vertebrae from all regions of the body with swellings on the neural arch roof on either side of the spine, forming short longitudinal ridges. Similar features in some *Wonambi* from Riversleigh are associated with small foramina (not the case here). Vertebrae similar to these and referred to *Nanowana* sp. (most of them probably *N. godthelpi*) from numerous sites at Riversleigh, including well-preserved examples from Wayne's Wok, Wayne's Wok 2, Mike's Menagerie, and Upper Site.

Vertebrae of the cloacal region (Fig. 8) proba-

bly from a single individual with short centrum, broad zygosphene, and condyle smaller than neural canal (regional features allowing increased flexibility in this region). Haemal keel smooth (lacking the median ridge of *Wonambi* spp.), not or barely projecting below the centrum posteriorly. Two largest vertebrae with paradiapophyses indicating articulated ribs, but on one side of one of them the articular surface is expanded and roughened suggesting an immobile cartilaginous attachment (i.e. transitional to fixed lymphapophyses). Three others with lymphapophyses (broken distally); another with stumps of cylindrical fixed ribs, possibly forking more distally.

***Nanowana schrenki* sp. nov.**
(Figs 9-12, Table 2)

MATERIAL. Holotype QMF31395, a right palatine from early Miocene Upper Site, Godthelp Hill. Other Material: Upper Site: Maxilla fragments QMF 31390, 31391, 31394. Mike's Menagerie Site: Dentary QMF31392 and vertebra QMF23043. Camel Sputum Site: Dentary QMF23051; maxilla fragments QMF23082, 31388.

TABLE 2. Measurements of *Nanowana schrenki* sp. nov., Friedemann Schrenk, holotype and referred jaw elements. Abbreviations as in Table 1, with addition of dd8 = depth of dentary at 8th alveolus.

QMF	31395	31394	23082
IND	U	U	M
ptl	4.7		
pal	2.5		
pln	3.8		
prw	2.5		
pcw	1.3		
prw	0.6		
pnw	0.6		
mpw		1.7	
nph		2.0	(1.0)
Dentaries			
QMF	23051	31302	
Ind	CI	MM	
ml	3	3	
dl	(16.7)	(7.1)	
dl5	13.7		
dl7	15.6		
dlr	12.6		
dl1		5.3	
dl3	9.3	4.1	
dl4	11.2	4.6	
dl6	8.3	3.5	
dl8	6.7		
dl9	2.3	1.0	
app	0.7	0.4	

view. Three mental foramina, the third posterior to the 7th tooth.

DESCRIPTION. Holotype. Alveoli 11, teeth ankylosed in 1, 3, 4, 5, 6, 8, 9, 10, 11; only 8, 10 and 11 complete. Teeth with a simple curve, directed posteriorly. Tooth row deflected slightly medially anteriorly, laterally posteriorly. Maxillary process slightly wider than the tooth-bearing bar, extending from between 2nd and 3rd to between 6th and 7th teeth, with an anteriorly sharp lateral notch, and sharp posterolateral angle. Ventral surface of the process with a diagonal ridge from the rear of the 4th tooth to the posterolateral angle, defining an anterolaterally concave facet to articulate with the palatal process of the maxilla. Anteriorly, the edge of the lateral process

continuous with a dorsolateral ridge extending to the anterior tip of the tooth-bearing process. A second ridge diverging medially from the anterolateral corner of the process, bearing a distinct knob above the tooth row and continuing onto the anterior edge of the choanal process, level with the rear of the 4th alveolus. Anteromedial corner of choanal process (to articulate with posterior process of vomer and possibly parasphenoid) missing. Medial edge intact, and smoothly convex, from level of 7th alveolus to rear of tooth row, but posterior process broken off. Cusp defining lateral edge of choanal trough diverging posteromedially from the 6th tooth, disappearing level with the 8th; 2 foramina close together in the space between and medial to 7th and 8th alveoli, one of them piercing the choanal plate to emerge dorsally in a more medial position and opening medially. Tooth-bearing bar pointed posteriorly, tapering from the 9th tooth, a broad parabolic surface for the retractor pterygoidei on the ventral face with its apex beside the 9th, becoming less distinct posterolaterally. Deep notch to articulate with the pterygoid on the dorsal side between the tooth row and posterior process, extending to above the anterior edge of the 10th tooth. Distinct growth lines through the translucent choanal plate parallel to its curved medial edge.

DIAGNOSIS. Lateral process of palatine about as long as 4 alveoli (3-6), with dorsolateral margin strongly notched; ventral ridge of palatine maxillary process without distinct angular concavity, matching smooth edge of maxillary palatine process. Maxilla estimated to have about 19 tooth positions; palatine with 11, pterygoid unknown, dentary 18 (or 17-18). Teeth ankylosed normally; 2nd to 4th of dentary, and 4th to 7th or 8th of maxilla, much larger than others. Dentary tooth row nearly straight in dorsal

view. Three mental foramina, the third posterior to the 7th tooth.

REFERRED MATERIAL. Maxilla represented by several fragmentary specimens from different sized individuals (Fig. 10). Tooth row curves medially anteriorly (QMF23082), with a strong gradient of increasing alveolar diameter from 1 to 5; 5 and 6 subequal. Dorsal edge is a sharp, concave dorsomedial crest, extending to a high dorsal process, levelling off above 6th alveolus; this crest divides anteriorly, enclosing a shallow trough above the first two alveoli (thus, maxilla partially flooring nasal cavity). Lateral face mostly convex, with a shallow longitudinal trough including a large foramen (opening anteriorly and ventrally) above rear of the 4th tooth; a smaller foramen near the dorsal edge above the 5th. Medial face concave, with a trough just below the dorsomedial ridge containing a small foramen just anterior to the medial one. Middle part of maxilla (QMF31394) with distinct knob-like posterior part of prefrontal process and sloping suborbital portion, becoming more rod-like and wider than high posteriorly. Tooth size decreasing sharply, with increased alveolar spacing, just behind prefrontal process; longest (7th or 8th?) 2.2mm long, curved at middle but straight

distally, with medial and lateral cutting ridges (like longest tooth of dentary QMF31392, see below); more posterior teeth (broken before drawing) with simple curve, about half as long. Palatine process diverging from tooth row at last large tooth and reaching maximum width between the next 2 alveoli. Medial edge of the palatine process quite smooth, matching the concavity of the maxillary process in the holotype; large opening on dorsal face of process for palatine nerve and blood supply through several foramina on lateral surface. Teeth on posterior part of maxilla (QMF31391) still reducing in size from anterior to posterior, and with slight double curve. Posterior part triangular in section, with near vertical lateral and oblique dorsomedial faces both slightly concave, meeting at a dorsolateral ridge. Lateral edge straight, medial edge produced as ridge with convexity probably marking anterior limit of ectopterygoid.

Dentaries. Two right dentaries, differing considerably in size (Fig. 11), represent the lower jaw in this species. QMF31392 with complete row of 18 alveoli, teeth ankylosed in 1 (possibly), 3, 6, 8, 10, 11, 13, 15, 16, and 18; 10th broken, other teeth in tact, and a replacement tooth apparently *in situ* behind 15th. QMF23051 has 17 alveoli, but another may have been present posteriorly; 1, 4, 5, 6, 7, 9, 11, 12, 13, 14 and 15 ankylosed, but all teeth broken near base (the jaw has also been broken through 3rd alveolus and subsequently healed in life). 1st alveolus approximately same size as 5th, but 2nd to 4th considerably enlarged; 3rd nearly twice diameter of 5th, size decreasing gradually more posteriorly; in the small specimen, lengths of teeth from anterior edge of base to tip (mm) -, -, 1.26, -, -, 0.61, -, 0.63, -, -, 0.55, -, 0.52, -, 0.40, -, 0.37, 0.28. Anterior alveoli (1-3) deflected ventrad and mediad relative to rest of tooth row, which is moderately concave dorsad

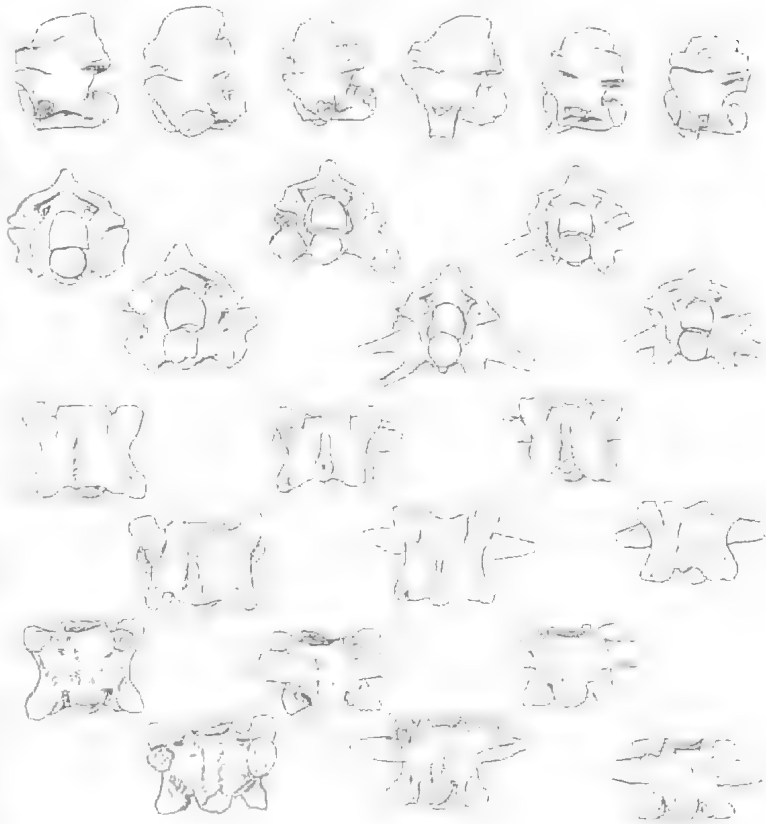


FIG. 8. *Nanuwana godthelpi* sp. nov., series of most posterior trunk and clacal vertebrae from Upper Site, possibly from the same individual as jaw elements in Fig. 6. Lateral, posterior, dorsal, and ventral views.

but only very weakly concave mediad. Third tooth directed slightly laterad as well as posteriad; other teeth mediad, more strongly towards the rear of the tooth row. Each tooth with a weak lateral and medial cutting edge near the tip. Dentary deepens gradually from anterior to posterior. Three mental foramina open anteriorly below alveoli 4, 7 and 9 (QMF31392) or 3, 6-7 and 8 (QMF23051), decreasing in size posteriorly. A shallow dorsal trough medial to 3rd and 4th alveoli defined by a dorsomedial crest. Lateral fossa extends as far anteriorly as the rear of the 13th tooth, blunt in outline; posterior edge of the vertical intramandibular septum smoothly concave, extending forward to between the 14th and 15th teeth. Differences between the two include shape of Meckel's groove (tapering more strongly in the small jaw, dorsal edge composed of two sharply defined sections separated by a short gap below 8th-9th alveoli, but no gap in the larger speci-

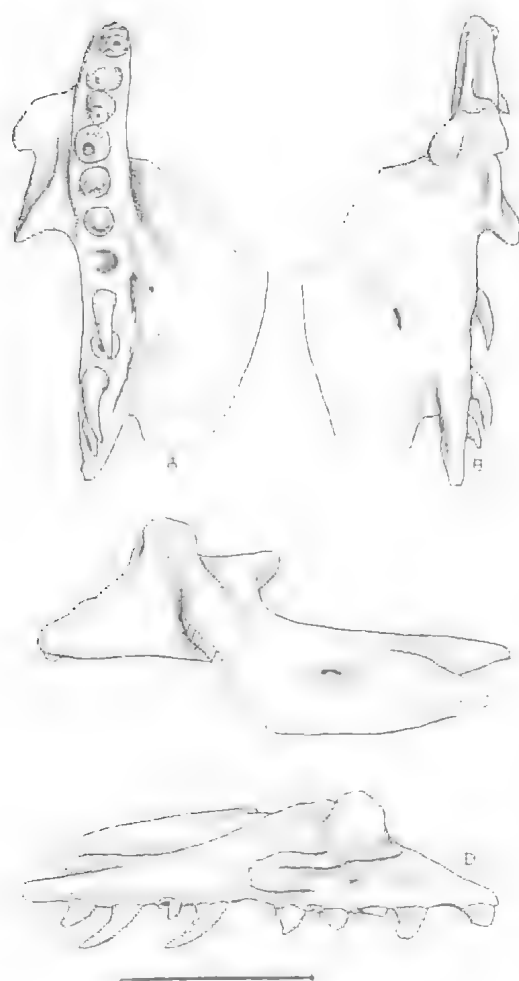


FIG. 9. *Nanowana schrenki* sp. nov., holotype, QMF31395 from Upper Site, palatine in ventral (A), dorsal (slightly lateral) (B), dorsomedial (C), and lateral (D) views. Scale bar=2mm.

men), upper facet for splenial (with posteromedial angle in the smaller, but a free-ending process in the larger), and lateral fossa (constricted in the smaller by deepened upper posterior process); both narrowest in the region of the 6th to 8th alveoli; but the larger specimen is relatively broader posteriorly.

Vertebra (Fig. 12) from mid-trunk of a juvenile, with short broad centrum, large neural canal, and condyle and cotyle much wider than deep. Weakly defined subcentral ridges narrow only slightly behind the parapophyses, posterior half of centrum nearly parallel-sided except for a shal-

low, short precondylar constriction. Blunt haemal keel extending from just behind the cotylar rim, posteriorly forming a slightly prominent single hypapophysis extending below the condyle. Keel defined laterally by broad shallow depressions. Comparisons with *Yurlunggur* or *Patagoniophis* would imply that a haemal keel of this form indicates a vertebra from close to the cardiac region (transitional between prominent single hypapophysis anteriorly and flattened or double keel posteriorly), and would thus be among the largest in the skeleton. Condyle and cotyle about twice as wide as deep, slightly oblique in lateral view; cotyle wider than the neural canal but not as wide as the zygosphen. Zygapophyseal facets inclined at less than 20° above the horizontal, defining planes which intersect near the middle of the neural canal. Prezygapophyseal facets obovate, with transverse anterior edge; postzygapophyseal facets more smoothly oval, and somewhat prominent posteriorly in dorsal view. Both pairs of facets are elongate anteroposteriorly, with long axes at about 35° to the sagittal plane (as in anterior, but not middle trunk vertebra of *Patagoniophis* sp. cf. *P. parvus*; Scanlon, 1993). No prezygapophyseal processes.

Paradiapophyses directed ventrolaterad, slightly wider than prezygapophyses, not extending ventral to cotylar rim. Interzygapophyseal ridge smoothly concave laterally, only slightly wider than the centrum, and weakly defined in lateral view.

Zygosphen thin, slightly arched; anterior edge smoothly but weakly concave (again, like anterior rather than middle vertebrae of *Patagoniophis*). Zygosphenal facet (preserved on left only) dorsoventrally shallow, with dorsally convex upper and lower edges, inclined at about 45° from vertical; a plane tangent to the facet would pass close to the centre of the neural canal.

Neural canal arched, about as high as wide, lacking internal lateral ridges. Neural arch low, with shallow concavities above and below the level of the zygosphen and extending to the posterior edge. Zygantral roof arched, thickness uniform across its width. In dorsal view, rear of neural arch forming a broad concavity above the zygantrum, interrupted by the neural spine. Low neural spine formed by a narrow, but sharply defined anterior lamina rising from the rear of the zygosphen and applied to a higher, columnar portion posteriorly, overhanging the zygantrum. Dorsal surface of column broken off, with a sinus visible within the neural arch. Lateral and sub-

central foramina present, any other obscured by dendrites.

TROPHIC SPECIALISATIONS OF *NANOWANA*

N. godthelpi sp. nov. The homogeneity in size, morphology and approximate stratigraphic position of these toothless but otherwise well-preserved jaws makes it appear probable that the lack of ankylosed teeth is a natural (and apomorphic) characteristic. To quote Owen's (1840) conclusion on the 'dislocated' tail of ichthyosaurs, the toothless condition '... is too uniform and common to be due entirely to an accidental and extrinsic cause'. Variation in the shape and size of alveoli along the tooth rows, and the presence of 'frothy' bone similar in some cases, indicates that different stages of replacement are represented, so that absence of teeth is not explained by synchronised replacement. Some of these specimens are practically intact, preserving delicate processes, and not worn in such a way as to account for the absence of even stumps of teeth; in most other specimens from the same deposits, parts of teeth are typically retained even after heavy wear. The alveoli are shallow, rather rectangular pits, so that a thecodont type of implantation is not indicated as an alternative to ankylosis.

Failure of teeth to ankylose at any stage is rare among squamates, first reported by Savitzky (1981). *Anomochilus weberi*, a small fossorial 'anilroid' (Anomochilidae is possibly the sister taxon to other

living Alethinophidia; Cundall et al. 1993), apparently has fibrous tooth attachment rather than ankylosis (Cundall & Rossman, 1993). There are also several lineages of snakes, and one genus of

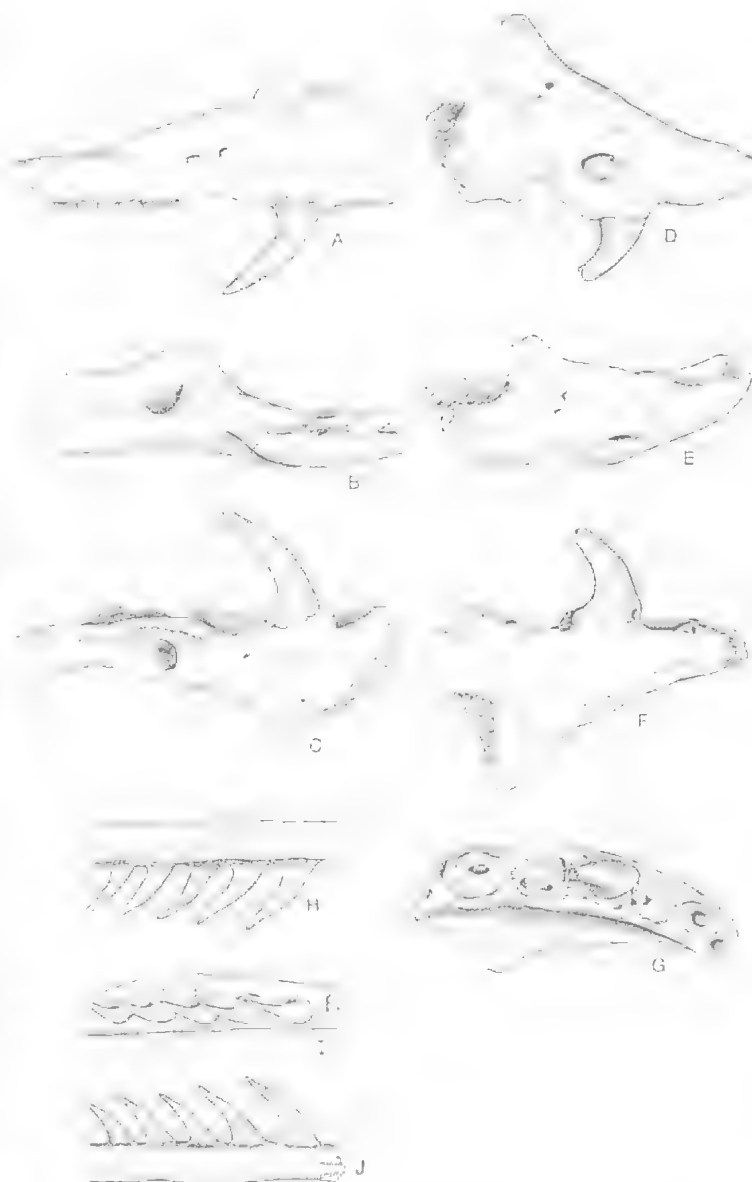


FIG. 10. *Nanowana schrenki* sp. nov., maxillary fragments. A-C, QMF31394, Upper Site, middle part of right maxilla in lateral, dorsal, and medial views. D-G, QMF23082, CS Site, anterior right maxilla in lateral, dorsal, medial, and ventral view. H-J, QMF31391, Upper Site, posterior left maxilla in medial, ventral, and lateral views. Not to same scale.

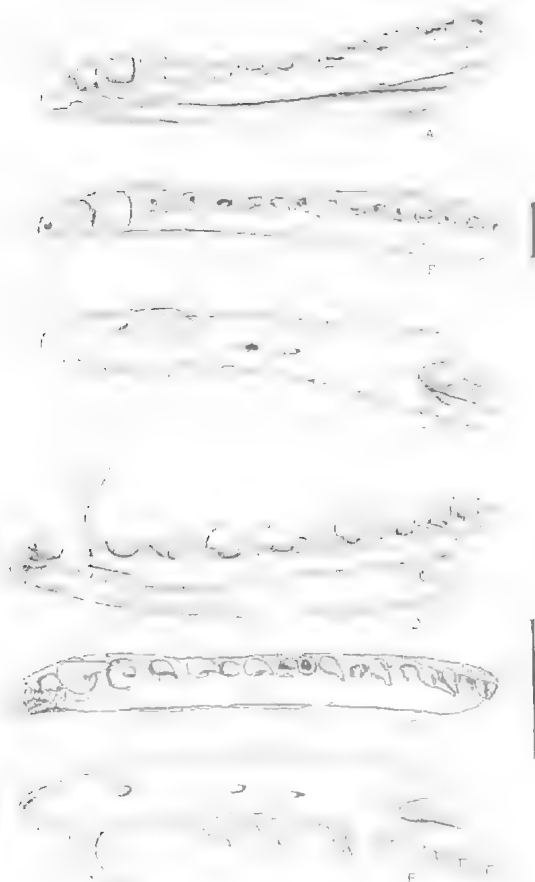


FIG. 11. *Nanowana schrenki* sp. nov., right dentaries. A-C, QMF23051, CS Site, in medial, dorsal, and lateral views. D-F, QMF31392, MM Site, in medial, dorsal, and lateral views. Scale bars=2 mm.

lizards, where the attachment is not only fibrous but forms a functional hinge allowing each tooth to fold posteriorly under pressure and return upright when released (Savitzky, 1981, 1983; Patchell & Shine 1986c; cf. Edmund, 1969:141). This hinge mechanism has been interpreted in each case as an adaptation to feeding on scincid or gerrhosaurid lizards in which the scales are underlain by osteoderms; the hinged teeth are

thought to act as a ratchet mechanism, folding back rather than penetrating the dermal armour, and locking in an upright position against the edges of the scales when the prey is oriented head-first for swallowing. In extant snakes other functionally associated apomorphies also occur; the teeth are small and numerous, often with a spatulate rather than conical tip, and lack enamel on the posterior surface; and the levator anguli oris muscle (inserting on a long upper posterior process of the dentary) is enlarged (Savitzky, 1981). In the pygopodid *Lialis* teeth are of similar form, and instead of increased intramandibular kinesis there is pronounced kinetic ability at the frontoparietal joint (mesokinesis; Patchell & Shine 1986b). Both types of kinesis allow the jaws more effectively to surround and compress a cylindrical prey item, immobilising or even asphyxiating it. An equivalent adaptation for prey-holding (without hinged teeth) is seen in the largely scincivorous bolyeriid snakes, in which the required kinesis is provided by the uniquely derived intramaxillary joint (Cundall & Irish, 1989).

Savitzky (1983) described this set of adaptations to feeding on skinks, which has evolved independently in several lineages, as an instance of a 'coadapted character complex', among other cases of 'durophagy' (feeding on hard-bodied prey). Other durophagous snakes have distinct specialisations, and feed on other kinds of 'hard' prey such as snails (pareine and dipsadine colubrids) or crabs (the homalopsine *Fordonia*). 'Durophagy' is thus a broad concept. I introduce 'arthrodonty' to refer specifically to the 'hinge-toothed' mode of durophagy.

While soft-tissue structures such as fibrous hinges cannot be observed in fossils, absence of ankylosis implies that attachment was fibrous and potentially flexible. *N. godthelpi* jaw material is similar to that of extant arthrodont species after maceration, especially *Xenopeltis* (Savitzky, pers. comm.). Hutchinson (1992) demonstrated that scincid lizards were abundant and diverse in the Tertiary at Riversleigh; skinks today represent a major food source for small terrestrial predators, including most extant Australian snake species (Shine, 1991). As functional arthrodonty has evolved in several lineages in association with predation on skinks, its presence in *N. godthelpi* is a plausible explanation for the lack of ankylosis.

N. godthelpi appears to be less specialised than each of the extant arthrodont snake lineages in some respects. The high number of nearly uni-

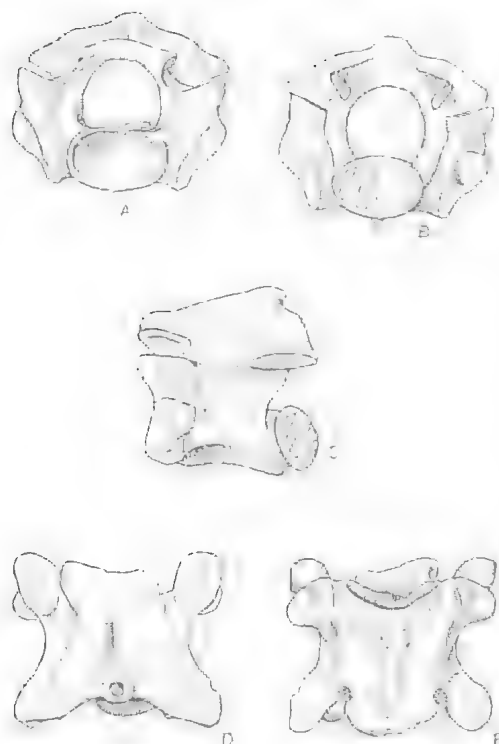


FIG. 12. *Nanowana schrenki* sp. nov., vertebrae, QMF23043, MM Site, probably same juvenile as dentary QMF31392 (Fig. 11) in anterior (A), posterior (B), lateral (C), dorsal (D) and ventral (E) views.

form maxillary alveoli is typical of an arthrodont species, but a similarly long tooth row is present in *Wonambi naracoortensis* (Barrie 1990), and is therefore likely to be a retained ancestral condition rather than a specialisation. The overlap between dentary and compound is moderate, without any great elongation of the tooth-bearing posterior process; the extreme condition in extant arthrodont lineages may be precluded by the probable insertion of *m. levator anguli oris* on the relatively large coronoid rather than the dentary, but the overlap is actually shorter in this species than in *Wonambi*.

The dentary alveoli of *N. godthelpi* are considerably larger, especially in the middle part of the row, than those of the maxilla, so the lower teeth may have functioned differently, and possibly lacked a functional hinge. In *Xenopeltis*, relatively large teeth are present on the middle part of the palate (posterior palatine and anterior pterygoid), but these appear to be fully hinged. While fibrous attachment of 'sessile' teeth has been

reported only in one highly unusual extant taxon, *Anomochilus*, it is possibly a necessary precursor or incipient stage of arthrodonty (see below), and a mixed or 'semi-arthrodont' condition in *N. godthelpi* seems possible.

Nanowana schrenki sp. nov. In the absence of articulated or strongly associated material, referral of jaw elements described here to a single taxon can only be provisional. In particular, the 2 near-complete dentaries differ in several respects which make their assignment to the same species doubtful: in QMF23051 the upper edge of the Meckelian groove is a continuous ridge and extends posteriorly as a free-ending process, while in QMF31392 it is interrupted at the 9th alveolus, and appears to end abruptly. (Additionally, the larger specimen broadens more posteriorly, while the small one is widest at the 3rd tooth, but this difference may be allometric.)

The teeth of snakes play several roles in the capture, subdual, puncturing or laceration, and swallowing of prey; in general they will be adapted for a combination of functions, but often either a single function is dominant, or certain stages are either not required (e.g. because inactive or defenceless prey is taken) or carried out extra-orally (e.g. constriction). Teeth specialised for different functions are often separated between the front and rear of the mouth, in some cases with diastemata between teeth of different morphology (Frazzetta, 1966; Scanlon & Shine, 1988; Cundall & Irish, 1989).

Numerous terms have been introduced for different patterns of tooth size and fang location (Smith 1952). Primitive snakes (*Dinilysia*, aniliids) are isodont or mesodont, with relatively few, stout teeth; while also capable of constriction, they use a powerful 'crushing' bite in subduing prey (Frazzetta, 1970; Greene, 1983). Such a 'crushing' method seems possible for *Madtsoidia* cf. *M. bai*, in which the dentary is heavily built and bears relatively few teeth (Hoffstetter, 1960), but not for Australian madtsoids. Different patterns of tooth-size variation in upper and lower jaws are known in each of the 4 best-represented taxa:

In *Wonambi naracoortensis* the very numerous teeth (25 in the dentary, 22 or 23 in the maxilla) are proterodont, sharp and strongly inclined posteriorly and medially (Barrie, 1990); the jaws are shallow, suggesting a limited role in subduing prey, and more emphasis on holding and swallowing functions. This implies that an extra-oral method of subduing prey (probably constriction) was well-developed. When the upper and lower

jaws are both proterodont, teeth often have a sigmoid curvature with the tips directed somewhat anteriorly as in many pythons (Frazzetta, 1966), and seems to be associated with relatively soft-bodied prey such as mammals, birds, earthworms (McDowell, 1969) and eels (Smith, 1926; Cogger et al., 1987).

Nanowana godthelpi apparently had a nearly isodont marginal dentition. No complete tooth crowns have been reported for this species, but based on alveolar sizes it was weakly proterodont on the maxilla and mesodont on the dentary (Figs 1, 3).

The condition in *Yurlunggur* is less clear but apparently the opposite; a dentary with well-preserved teeth (Archer et al., 1991:71) is proterodont, while the maxilla was apparently mesodont (Scanlon, 1996).

N. schrenki can be described as megadont (Smith, 1952), having regions of distinctly enlarged teeth. Otherwise it has the same pattern of enlargement as *Yurlunggur*, opposite to that of *N. godthelpi*, being mesomegadont on the maxilla and promegadont on the dentary. The dentary is relatively longer and less robust than in *Madtsoia* or *Dinilysia*, but not depressed as in *Wonambi*; the teeth are intermediate in number and in morphology (stouter and more erect than *Wonambi*, but not so much as in *Dinilysia* or anilioids); and the enlarged teeth are a uniquely derived condition within Madtsoiidae (albeit convergent with many other lineages of snakes).

Many snakes share this pattern of enlarged teeth at the front of the dentary and the part of the maxilla below the prefrontal articulation, whether or not they are set off by diastemata or local minima of tooth size. On the basis of occurrence in scincivorous colubroids such as *Lycodon*, *Glyphodon*, *Demansia*, and *Hemiaspis signata* (but not the anurophagous *H. dameli*; Boulenger, 1896; Worrell, 1961; Shine, 1991; Cundall & Irish, 1989; pers. obs.), this is here tentatively considered an adaptation to hard-bodied prey, often skinks. Snakes with enlarged teeth offset between upper and lower jaws are able to trap hard, cylindrical prey items between a notch in one tooth-row and one or more enlarged fang-like teeth (sometimes true fangs) in the other (Cundall & Irish, 1989). As well as this 'trapping' function, having only a few long teeth in each jaw maximises the probability of hard-bodied prey being deeply punctured, whereas this is avoided in arthrodont forms.

EVOLUTION OF TEETH AND ATTACHMENT

Snake teeth are slender compared to other vertebrates; they break frequently during normal use and are quickly replaced (Edmund, 1969). They have reduced occlusal area (sacrificing strength) to increase sharpness and depth of penetration. Tooth form is a compromise between competing selective forces defining a 'fitness landscape' over attainable phenotypes (Wright, 1932), and local optima will be attained only if intermediate states are evolutionarily stable. If the rate of breakage is too high, prey capture or swallowing efficiency (and consequently fitness) will be low.

During the stages of feeding on a given range of prey types with given neuromuscular repertoires, forces on the tooth come from particular directions with greater or lesser frequency and magnitude, so it will generally be favourable for the tooth to be asymmetrical rather than a simple cone. The orientation of 'cutting ridges' (which function as buttresses as well as blades), curves in the shaft, and the shape of the tooth base, will confer maxima of resistance in one or more directions, at the expense of minima elsewhere.

Horizontal components of pressure (shear stress) at the tip of an approximately conical tooth are converted to bending stresses at the base, i.e. compression at one side and tension at the other. The magnitudes of these forces will depend on base diameter, but only tension and shear will tend to either break the shaft or disrupt the attachment of tooth to bone. Bone of attachment can apparently withstand such stresses within a wide range of values of the ratio of tooth length to basal diameter. A fibrous connection will remain stable at low values of this ratio (short, broad teeth as in *Anomochilus*), and at intermediate values will have enough elasticity to return the tooth upright after displacement (functional arthrodont condition). At high values (longer, slender teeth) a fibrous attachment would merely bend passively, without developing enough tension to right the tooth; the orientation of the teeth would then not be precisely controllable, and during prey capture and ingestion they would more often encounter shear stresses at unfavourable angles, leading to rupture. Such a condition (elongate, slender teeth with fibrous attachment) is unknown in any living snakes, and would presumably be evolutionarily unstable for most diets and feeding methods.

This consideration of the forces applied at the tooth tip and base suggests that arthrodonty and elongate teeth are mutually exclusive conditions.

Thus the specialisations of dentition and jaw morphology in *Nanowana* are most likely to be independently derived from the nearly isodont, ankylosed condition of other madtsonids, and apparently represent alternative solutions to the problem of feeding on hard-scaled lizards.

Healed breaks of the jaw elements (particularly dentaries) are not uncommon in snakes (pers. obs.), and presumably result in most cases from attempts to capture or subdue relatively large and powerful prey. Sublethal trauma associated with particular morphological specialisations may be an indicator of mechanisms of selection; there are upper limits to prey size and strength for every species of predator, and both prey selection and behavioural aspects of prey-handling, as well as morphology, will be subject to selection. The break through the third dentary alveolus of QMF23051 (*N. schrenki* sp. nov.) would have occurred most easily (i.e. greatest stress would occur) while the 3rd alveolus was unoccupied, and while a prey item was held by the enlarged 2nd tooth, but not the smaller posterior teeth. Fractures of this kind could be expected to be less common (all else being equal) with a more uniform dentition, but this possible disadvantage of megadonty may have been outweighed by an increased rate of capture success, or of retention once a prey item was secured behind (or impaled on) the enlarged dentary teeth.

The ribbon-like posterior maxilla of *N. godthelpi* presents an even more fragile appearance, but no specimens suggest breaks during life. While this is negative evidence, the rarity of such breaks would tend to support the presence of a jugal in the suborbital region. Presence of a jugal in *Wonambi naracoortensis* can similarly be inferred from the oblique trough crossing the maxilla (Barrie, 1990; Scanlon, 1996) which would otherwise be an obvious point of fragility.

SYMPATRY OF RELATED SPECIES WITH SIMILAR DIETS

The two species of *Nanowana* occur together in at least 3 Sites, existing sympatrically for a significant period. They are thought to have had similar diets (skinks), and similar adult size. They thus occupied quite similar niches, and were strictly equivalent ecologically. They may have differed in aspects of behaviour which would not be discernible in the fossil record, but at least a difference in habitat can be suggested.

The different representation of the two species when found together (minimum number of indi-

viduals, number of identifiable elements, and quality of preservation) implies that *N. godthelpi* was more abundant close to the sites of deposition, whereas *N. schrenki* may have been less abundant locally, and the more damaged remains transported from further afield (cf. LaDuke, 1991). Thus *N. godthelpi* lived near water (possibly riparian, probably closed forest), whereas *N. schrenki* may have lived further from water, possibly in more open or drier areas such as clearings or rocky hills.

Most sites where *Nanowana* vertebrae have been found have not produced jaw elements diagnostic to species. The genus as defined here, therefore provides a convenient level of description which can be applied to a larger set of sites, but as yet all specimens referred to *Nanowana* are from Riversleigh.

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CAINOZOIC TURTLES FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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The Chelidae and Meiolaniidae occur in the Oligo-Miocene at Riversleigh with the former dominant and short-necked *Elseya/Emydura* accounting for over 90% of turtle material. *Chelodina* and *Pseudemydura* are present with several undescribed forms. Chelid diversity increased from the Oligocene to the Miocene, while average size decreased, suggesting a change in the aquatic habitats. I propose that large late Oligocene river and overflow systems were replaced by smaller, slower-flowing waterways that by the mid-Miocene had developed numerous small, stationary aquatic habitats, some occupied by dwarf turtles.

The Miocene appearance and radiation of the large terrestrial meiolaniid turtles and their presumed thermal and dietary requirements suggest that Riversleigh's gallery forests were heterogeneous and punctuated by open clearings. Absence of trionychid turtles and dearth of long-necked chelids may be related to the general unsuitability of habitats at Riversleigh, particularly during the Oligocene. □ *Australia, Riversleigh, turtles, palaeoecology.*

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Riversleigh's Oligocene and Miocene turtles (White, 1988, 1990, 1992; Gaffney et al., 1989; White & Archer, 1989) represent the highly aquatic side-necked Chelidae and the large, terrestrial, horned Meiolaniidae.

Chelid remains are common in Systems A, B and C of Archer et al. (1989, 1994) and are known from Pleistocene gravels (Terrace Site) adjacent to the Gregory River (White & Archer, 1994). Living specimens of the presumed extinct *Elseya lavarackorum*, have been collected from nearby Lawn Hill Creek and subfossil material from near the Gregory River (Thomson et al., 1997). Meiolanid remains are confined to System B and one site in System C (Gaffney et al., 1992).

Riversleigh turtle material including skulls is well preserved (White & Archer, 1993) but no articulated remains have been found. Relationships of extant chelids have been based almost exclusively on cranial anatomy (Gaffney, 1977, 1979) but biochemical techniques are establishing alternative phylogenies (Georges & Adams, 1992) and derived shell features have been used to define fossil species (White & Archer, 1994).

FAMILY CHELIDAE

The extant chelids *Pseudemydura*, *Emydura/Elseya* and *Chelodina* have been reported from the Oligocene-Miocene of Riversleigh (White, 1988; Gaffney et al., 1989; White & Archer, 1989).

Chelid taxonomy is based heavily of features of the skull (Gaffney, 1977, 1979). There are no derived skull characters known that can be used to distinguish *Emydura/Elseya* despite these genera being electrophoretically distinct (Georges & Adams, 1992). Shell features are not normally used because they have been presumed to be variable in chelid lineages (Gaffney, 1977) but some diagnostic shell features are now known (White & Archer, 1994; Thomson & Georges, 1996). I adopt the more conservative position of using skull features to distinguish short-necked chelids. Gaffney et al. (1989) reported on *Emydura/Elseya* skull material from Riversleigh although shells and shell pieces were available. Scute features are used to identify modern taxa but these have little or no phylogenetic value (Gaffney, 1979).

Riversleigh Oligocene-Miocene turtles are dominated, both in abundance and diversity, by short-necked chelids of which *Emydura/Elseya* were most common (White & Archer, 1989), representing over 90% of identifiable material, and are known from 10 fossil sites. These two genera contain nearly 60% of extant chelid species (Georges & Adams, 1992). Two mandibular pieces from Riversleigh's Bob's Boulders (System C) are the only remains assignable directly to *Elseya*. They have alveolar ridges typical of the *Elseya dentata* species complex.

A single skull fragment and partial plastron of *Pseudemydura* is known from Ringtail Site (System C; Gaffney et al., 1989). This genus contains

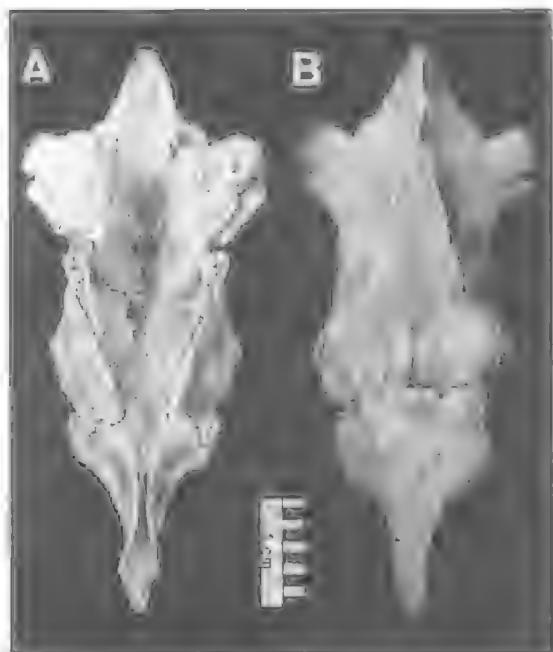


FIG. 1. Skull of *Chelodina* sp., QMF31303, Quentin's Quarry, Riversleigh. A, dorsal. B, ventral.

a single extant species, the Western Swamp Tortoise (*P. umbrina*), an endangered species confined to two small swamps north of Perth (Cogger, 1992). The Riversleigh specimen is the first fossil record of the genus and indicates *Pseudemydura* was once much more widespread. *Pseudemydura* is the most derived extant chelid (Gaffney, 1977, 1979) and is unusual among pleurodires in having little temporal or posterior emargination of the skull. This results in a skull with a near complete roof above the cranium. The Riversleigh skull fragment consists of a massively expanded supraoccipital indicating that enclosure of the hindmost portion of the skull occurred before the Miocene. Similarity of the Riversleigh specimen to the modern species suggests that *Pseudemydura* diverged from other short-necked chelids early in the Australian radiation, a conclusion supported by cladistic analysis of modern chelid skull features (Gaffney, 1977). Electrophoretic data (Georges & Adams, 1992) did not include *Pseudemydura* and Gaffney's (1977) hypothesis that *Pseudemydura* is the sister-group to all other Australian chelids remains (but see Manning & Kofron, 1996).

Long-necked chelids arose before the Oligocene (Manning & Kofron, 1996). Georges & Adam's (1992) indicate that *Chelodina* is the sister group to all Australian short-necked turtles

(excluding *Pseudemydura*). An almost complete plastron and some carapace bones of a small long-necked *Chelodina* are known (Gaffney et al., 1989). A species of *Chelodina* from Quentin's Quarry Site is described below. An almost entire carapace of a diminutive chelid from Melody's Maze Site (System C) and a partial skull from CMP Site (System C) White (1992, 1993) are described below.

SYSTEMATICS

Order TESTUDINES Linnaeus, 1758
 Infraorder PLEURODIRA Cope, 1863
 Family CHELIDAE Gray, 1825
 Subfamily CHELINAE Gray, 1825

Chelodina sp. (Fig. 1)

MATERIAL. QMF31303, dorsal skull elements consisting of a fused frontal, paired parietals and prootics and supraoccipital bones from Quentin's Quarry Site, middle Miocene, System C.

DESCRIPTION. Frontal fused, detached from parietals, with suture undamaged. Posterior tip of supraoccipital missing. Parietals joined, sutured to their respective prootics and the supraoccipital. Frontal flat, roughly triangular, with maximum width behind rim of the orbit near the suture for the postorbital bones, with long and tapered anterior aspect, with the suture for the prefrontal as well as the rim of the orbit. Suture with the parietals horizontal. Parietals wider than frontal at their suture, widest in the posterior section of the orbit near their sutures with the postorbital bones, with dorsal aspect drawn into a tapering sagittal crest terminating with the intrusion of the supraoccipital to form the very tip of the crest. Supraoccipital forming roof of the posterior cranium; parietals forming roof for the majority of the vault. Cranium widest near the parietal-prootic suture. Prootics large, inflated, with suture attachments for the quadrate and basisphenoid intact, with latter suture uniting a broad foot-like plate of the quadrate with the basisphenoid.

DISCUSSION. This specimen is referred to *Chelodina* on the basis of the fusion of the frontal bones, absence of temporal skull roofing and lack of contact between the parietals and squamosals (Gaffney, 1977). Goode (1966) and Legler (1985) divided *Chelodina* into: the *C. longicollis* group (A) containing *C. longicollis*, *C. steindachneri* and *C. novaeguineae* and the *C.*

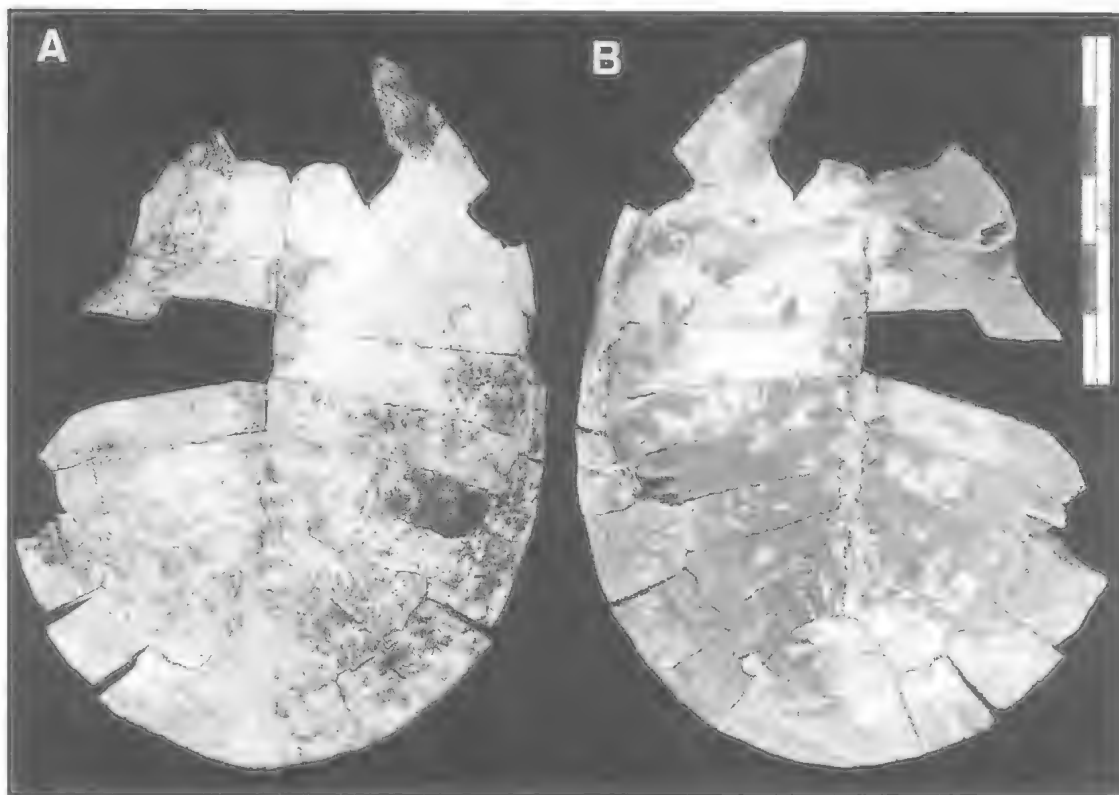


FIG. 2. Carapace of small turtle, QMF31304, Melody's Maze, Riversleigh. A, dorsal. B, ventral.

expansa group (B) containing *C. expansa*, *C. rugosa*, *C. oblonga* and *C. parkeri*. Goode (1966) separated short-necked species (Group A) where neck length is less than shell length, the posterior skull is not disproportionately extended, the basioccipital is large and expanded anteriorly, while the squamosal is reduced and lacks a protruding lateral process. Group B long-necked turtles were longer-necked where neck length is often longer than shell length, the posterior skull is markedly elongated, the basioccipital is small and squarish, and the squamosal has a prominent lateral process. Electrophoretic data (Georges & Adams, 1992) support these groupings but not their generic status. In particular, they disagree with the placement of *C. oblonga* and its relationship to the *C. longicollis* group.

The Quentin's Quarry shell cannot be readily allocated to either group although the skull shows no marked posterior elongation. The skull is unique in: 1. Contribution of the frontal bone to the orbit. In living *Chelodina* frontals are fused, forming a flat, dorsal plate behind the orbit with a thin medial process extending to the nasal re-

gion. The anterior process is intimately fused to the prefrontals which make up most of the dorsal orbit. The Quentin's Quarry skull has a thin medial process but the suture points with the prefrontals are minimal and anterior. The frontal process bears the rim of the orbit behind the prefrontal sutures and makes up the majority of the dorsal orbit. This means that the eyes were relatively closer together and directed more upwards than sideways. 2. Expanded anterior parietals. In modern long-necked turtles the anterior parietals are flat dorsally but curve steeply down to form the walls of the anterior cranium. In the Riversleigh specimen, there is a parietal shelf formed by the extension of the parietals. The postorbital bones are fused to this shelf which forms part of the roof of the post-orbital canal). 3. Triangular sagittal crest. In extant long-necked turtles the parietals are flattened dorsally before being drawn into a narrow, elongate mid-cranial crest that extends to the rear of the skull. This leaves a massive canal for the neck and jaw musculature. In the Quentin's Quarry skull, the dorsal parietals taper evenly to the back of the skull creating the most

robust crest of any known *Chelodina*. 4. Enlarged prootic bones. In modern *Chelodina* the prootics are fused laterally to the parietals. As such, they form a horizontal beam connecting the cranium to the external ear. In the Quentin's Quarry specimen the prootics are inflated producing a gradual sloping from the side of the skull down to the quadrate. The temporal canal is therefore triangular in profile with the majority of the canal space being more lateral and closer to the quadrate. 5. Restricted posterior extension of the skull. All modern long-necked turtles have low, elongate skulls. This is achieved by the extension of the mid and hind skull regions in the horizontal plane. In particular, the supraoccipital, quadrates, squamosals and opisthotics are markedly elongated. The Quentin's Quarry skull has an almost rectangular supraoccipital that would scarcely have extended beyond the external ear. 6. Shape of cranial vault. In modern *Chelodina* the cranium is widest near the frontal-parietal suture. In the Riversleigh long-necked turtle, the vault is widest in the mid-parietal, close to the prootic contact zone.

Genus indet. A
(Figs 2, 3)

MATERIAL. QMF31304, an almost entire carapace and right femur from Melody's Maze, Gag Plateau, Riversleigh, System C, middle Miocene (Archer et al., 1989).

DESCRIPTION. Carapace elongate, oval, 100mm long, 75mm wide across pleurals 4. Shell without keeling along the midline, lacking serrated posterior peripherals, relatively low and flat in profile, with a longitudinal vertebral depression running the length of the shell, without fenestra. Pygal without division or indentation. Pleurals 11, relatively small. Peripherals increasing in size towards the posterior, with peripherals 8 and 9 the largest; peripherals 3, 4 and 5 and part of 6 curved ventrally, forming rounded shell margin associated with the bridge; anterior and posterior to the bridge, peripherals flattened, forming lateral platforms around the shell. On the inside of the carapace, rib heads on each of the pleurals. Pelvic scars well-developed on pleurals 8 and the suprapygial bones. Transverse ridge running across the floor of pleural 1 from the raised rib head to the recess for the bridge. Recess curved anteriorly, meeting the peripherals near the suture between peripherals 2 and 3.

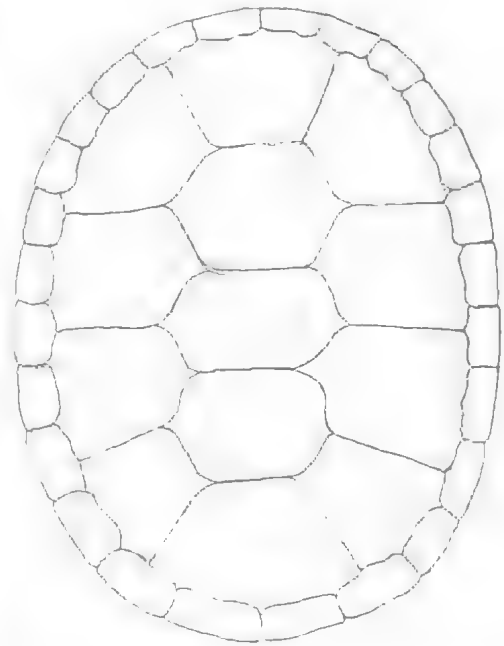


FIG. 3. Scute boundaries (dorsal) of QMF31304, turtle carapace from Melody's Maze.

DISCUSSION. The carapace has almost all of the right side intact, lacking only the third peripheral and nuchal bones. The left side is damaged and lacks peripherals 1 to 7 and portions of pleurals 1, 2 and 3.

The Melody's Maze carapace may be tentatively assigned to *Emydura* on the curved bridge recess and raised transverse ridge running across the floor of the first pleural bone (White & Archer, 1994). However, the pelvic scars on pleurals 8 and the suprapygals are more typical of *Elseya*. The shell is very small although it is from an adult animal. Its adult features include the closure of the carapacial fenestral, the tight fusion of the peripherals to the pleurals and the absence of features such as keeling of the carapace and expansion and flaring of the peripherals. The shell shows signs of advanced age: the extended growth of the pleurals during adult life has created a vertebral groove running the length of the carapace.

This shell cannot be placed in any of the known species of *Emydura* because of its small adult size and the unusual formation of the mid-peripheral bones. Among extant *Emydura*, the smallest known adults are in *E. signata* (Cogger, 1992) from the coastal rivers of northern NSW. Adult *E. signata* from the MacLean River show similar

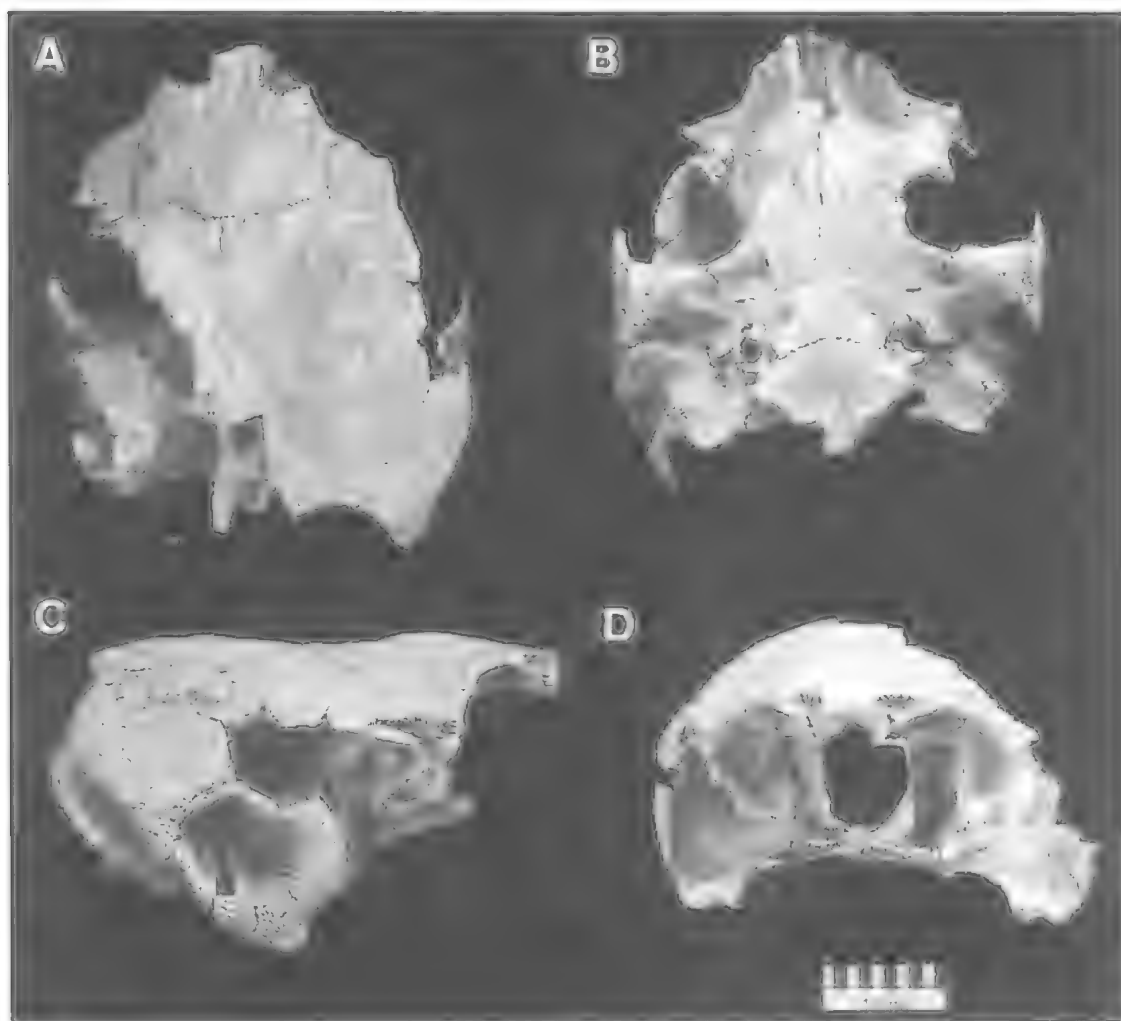


FIG. 4. Turtle skull, QMF31305, CMP Site, Riversleigh. A, dorsal. B, ventral. C, right lateral. D, posterior.

features to those of the Melody's Maze shell with carapace lengths of approximately 150mm.

Curving of the mid-peripheral bones associated with the bridge occurs elsewhere only in *Elseya dentata*-like turtles. In modern short-necked turtles, the peripherals are flattened and project laterally to form distinct ledges around the shell margin. The posterior peripherals are often flared to produce 'wings' that cover the hind limbs. There is virtually no flaring of the peripherals in the Melody's Maze shell; the peripherals are small compared to the pleurals (an adult growth trend in all chelids exaggerated in this species). Peripherals make up only 14% of the dorsal surface of the mid-carapace whereas *Emydura* (e.g., *E. krefftii*) the peripherals account for 20%.

The flattened shell is unlike most *Emydura* species which have domed shells. Only in *Pseudemydura*, *Chelodina*, *Elseya latisternum*-like turtles and some *Elseya dentata*-like species are the shells flattened and the central crest lost.

Genus indet. B
(Fig. 4)

MATERIAL. QMF31305, a partial skull comprising the paired frontals, parietals, post-orbitals, quadrates, right squamosals and supraoccipital, with paired pterygoids, quadrates, prootic bones, opisthotic bones, exoccipitals, basisphenoid and basioccipital from CMP Site, Gag Plateau, Riversleigh, middle Miocene, System C.

DESCRIPTION. Medium-sized, with extensive dorsal roofing, lacking temporal and posterior emarginations that typify most chelids (Gaffney, 1979a). Parietals expanded, forming the bulk of the dorsal roof; squamosals broad, forming the temporal bridge; supraoccipitals only contributing to the mid-dorsal section of the skull roof, weakly expanded in the dorsal plane.

Frontals paired, with small, anterior, medial projections dividing the prefrontals, contributing minimally to the hind orbit. Postorbitals mainly in the dorsal plane, with a descending strut forming the posterior wall of the orbit. Sutures for the jugal evident. The descending strut from the postorbital and ascending process from the pteryoid in broad contact. Alary process of the pterygoid reduced, may not descend ventrally below the level of the palate. Postorbital canal correspondingly more obvious in lateral view.

Dorsal skull sloping downwards anteriorly. Squamosal broad, forming a broad temporal arch between the quadrate and the parietals. Quadrate large, with a deep angular ventral base continuous with the articulation facet for the lower jaw. Quadrate with a deep posterior vertical groove.

Floor of the skull widening markedly where the parietals sweep laterally to unite with the quadrates. Articulation facet for the lower jaw well below the level of the palate, with a broad area formed by the lateral extension of the pterygoid and the quadrates. Pterygoids with a transverse suture with the palatines. Basisphenoid triangular, with a broad sutural contact with the basioccipital. Occipital condyle below the level of the foramen magnum.

DISCUSSION. The right side of the skull is relatively intact whereas the left parietals and squamosals are broken. The skull is heavily impregnated with a dark mineral.

The CMP skull cannot be assigned to any known infraorder or genus. It is particularly unusual in the structure of the skull roof. The only other chelid that lack posterior and temporal emarginations on this scale is *Pseudemydura* in which the roof is extensive, the posterior emargination is replaced by a posterior dorsal extension of the supraoccipital, and the temporal emarginations are replaced by the extension of the squamosal. In the CMP skull, the supraoccipital forms relatively little of the skull roof and some posterior emargination is evident. The squamosal is expanded, as in *Pseudemydura*. As a consequence, the temporal roof is broad.

In *Pseudemydura*, expansion of the supraoccipital causes the hindmost portion of the skull to be lower than the parietals. In the CMP skull, the parietals extend back to the posterior margins of the skull and overlie most of the supraoccipital. This results in the skull having an anterior slope with its highest point behind the level of the quadrates.

The quadrates have an unusually deep ventral footing that forms a thick foundation for articulation with the lower jaw. The articulation facet is dislocated laterally and lies beneath the most lateral edge of the quadrate. These features, combined with the reduction of the alary process of the pterygoid indicate an unusual distribution of muscles between the upper and lower portions of the skull. The ventral portion of the cranium and the exoccipital regions are very similar to the arrangement found in all Cheloniinae.

PALAEOECOLOGY

Living Australian freshwater turtles have a variety of life history strategies and survival mechanisms (Kennett et al., 1993; Grigg et al., 1986; Georges, 1982; Georges et al., 1986; Georges & Kennett, 1989; Heaphy, 1990; Kennett & Georges, 1990; Georges, 1988; Thompson, 1988).

Several major trends which may have ecological significance are apparent in Oligocene-Miocene turtle assemblages at Riversleigh. Only 2 families, the Chelidae and Meiolaniidae are present and of these, chelids make up about 98% of material recovered. Chelids dominate these fossil assemblages in the same way that they dominate modern Australian freshwater systems (Legler, 1985). Only in a few, far northern localities are non-chelid freshwater turtles present; *Carettochelys insculpta*, the Pig Nose Turtle (a carettochelid), is found in a few NT rivers (Georges & Kennett, 1989; Heaphy, 1990). The earliest Chelids known are from the Cretaceous of Patagonia (de Broin, 1994) and the family is thought to have evolved in southern Gondwana (South America and Australia). A sister-group, the pelomedusids, evolved at the same time in northern Gondwana and fossils occur in Africa, Madagascar and South America.

Other turtles lived in Australia during the Oligocene-Miocene including the giant horned meiolaniids and soft-shelled trionychids (Gaffney, 1979, 1981).

Another feature of the Riversleigh fossil turtle fauna is the dominance of the plesiomorphic short-necked chelids. *Emydura/Elseya* turtles ac-

count for over 85% of turtle remains. Modern *Emydura/Elseya* are predominantly herbivorous and occur in coastal and inland rivers, creeks and lagoons, especially those with a well-developed aquatic flora (Cann, 1978; Legler, 1985). They are not abundant in muddy or stagnant water.

Chelids in System A are typically large with shells up to 500mm long and equivalent in size to the largest extant chelids. Chelid fossils from Systems B and C are smaller (shell lengths 200–300mm) and thinner-shelled. System C turtle is a dwarf with adult shell 100mm long. The large System A turtles occur at Site D (Archer et al., 1994) which yields many broken sections of unusually thick turtle shell. Carapacial plates 10–20mm thick are typical. From the larger shell pieces I estimate shell lengths of 350–450mm.

The largest extant chelids are the northern snapping turtle (*Elseya dentata*) and gulf snapping turtle (*Elseya lavarackorum*) which inhabit large flowing rivers or deep still water bodies (Cogger, 1992). The only other fossil chelids from Riversleigh that approach the dimensions of the System A turtles are late Pleistocene Terrace Site (White & Archer, 1994).

Species diversity increases from Systems A to C with 1 chelid species in System A, 2 chelids and 2 meiolanids in System B and 6 chelids and 1 meiolanid in System C. The increase in diversity suggests an increase in small, shallow or slow-flowing aquatic habitats from late Oligocene to middle Miocene.

Maximum turtle size is a useful indicator of water depth and flow rate. Riverine species that occur in deep or relatively fast-flowing water are typically large and capable of sustained swimming. Smaller species are excluded from such sites and often confined to fringe water bodies such as side-streams, overflows or ponds (Pritchard, 1979). The range of small-shelled chelids in System C sites suggests that a variety of shallow water or slow moving habitats were available at the time. System C turtles typically had shell lengths 150–250mm.

The smallest extant turtle is the bog turtle, *Clemmys muhlengeri*, an emydid (Pritchard, 1979) which is 76–114mm long. These turtles occur in extremely shallow, still water habitats; in some cases free water is not available. None of these sites are necessarily clear water sites (Behler & King, 1979).

In the Gregory River at Riversleigh there are 5 chelids; these, in order of abundance, are *Emydura* sp. aff. *subglobosa*, *Emydura* sp. aff. *victoriae*, *Elseya latisternum*, *Elseya lav-*

arackorum and *Chelodina rugosa*. The latter two are uncommon. This level of diversity is reasonably high for modern freshwater habitats in Australia. Species diversity increases as mean temperature and habitat variation increase (Obst, 1986).

Only Systems B and C contain large, terrestrial turtles (meiolanids) with shell lengths up to 1 m long. Using *Meiolania platyceps* as a model, these creatures would have had average body masses of 150–200 kg.

There are a number of large, land turtles alive today. The best known are the various Galapagos tortoises (*Geochelone elephantopus*) and the Aldabran tortoise (*Geochelone gigantea*). Both reach body sizes and masses considerably greater than that calculated for Riversleigh's Miocene meiolanids. They are regarded as examples of island endemism leading to gigantism (Pritchard, 1979). The majority of the extant large terrestrial turtles inhabit hot savanna regions of the world. For example, both species of large African land turtles (*Geochelone sulcata* and *G. pardalis*) occur in northern and central Africa. Neither species is found in dense forest. *G. sulcata*'s distribution is along the southern Sahara into central Africa (Pritchard, 1979). Savannah habitat verging onto treeless plains is the preferred habitat for all African land tortoises.

During the Miocene, Riversleigh was covered by wet forest communities (Archer et al., 1994) but the large land turtles seem incongruous in this habitat. Land turtles such as the South American *G. denticulata* and *G. carbonaria* are generalist herbivores and live in a range of habitats, including open savanna, closed woodland and rainforest (Bjorndal, 1989; Moskovits, 1985; Moskovits & Kiester, 1987). While both species will venture deep into rainforest and feed on fungi, fallen fruit and herbs, they do not permanently reside in the closed forest. Both prefer to reside near the forest-savanna interface (Moskovits & Bjorndal, 1990). Flowers and grasses form a major part of the diet of South American land turtles in savanna and swamp habitats. They consume sand which is thought to assist digestion of coarse fibrous matter; they are hind-gut fermenters and need a certain amount of fibre in their diet. In the rainforest, the turtles get fibrous foodstuffs in the form of vines and shoots, but these are usually not plentiful. In addition, the tortoises seek out clearings (e.g. sites of recent tree falls) to bask. Hind-gut digestion requires fairly high and constant temperatures (of 30° or more) and the turtles need to have periodic access to direct sunlight. Youn-

ger and smaller turtles need access to sunlight on a more regular basis than large adults (Moskovits, 1985).

If these limitations for giant land tortoises apply also to meiolanid turtles living in or near forested habitats, then there must have been clearings where the animals could get sufficient volume of high fibre food and have direct access to sunlight. The round body form of these land turtles means that large animals would have a high thermal inertia. At air temperatures above 30° they may not need to seek additional external heat sources. However, should their body temperature fall below this level they would need to reach exposed sites quickly to restore core temperatures (Swingland & Frazier, 1979).

Riversleigh's meiolanids are low in abundance despite their high diversity; 4 species in 2 genera are known from 5 individuals. Chelids, in contrast, are represented by hundreds of specimens. Nothing is known about dietary requirements of horned turtles. Large extant terrestrial turtles are opportunistic herbivores and have requirements for fibrous matter intake (Pritchard, 1976). The unusual structure of the jaws of meiolanids indicates that some dietary selectivity may have been possible, but the nature of their diet is unknown.

The absence of soft-shelled trionychids from Riversleigh's Oligocene-Miocene coupled with the very low occurrence of long-necked turtles may be ecologically significant. Both types of turtles are 'ambush predators' (Pritchard, 1976). Both groups flourish in situations where they cannot be easily seen and this usually means turbid, muddy or dark water. Their absence and the preponderance of *Emydura/Elseya* suggests relatively clear water aquatic environments. *Chelodina* in System C coincides with the reduction in average chelid shell size, indicative of shallow, turbid lagoons during this period of the Miocene. The complete absence of trionychids suggests that the lagoons did not have silty bottoms and were unsuitable for concealment.

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NEW CROCODYLIANS FROM THE LATE OLIGOCENE WHITE HUNTER SITE, RIVERSLEIGH, NORTHWESTERN QUEENSLAND

PAUL M.A. WILLIS

Willis, Paul M.A. 1997 06 30: New crocodilians from the late Oligocene White Hunter Site, Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 423-438. Brisbane. ISSN 0079-8835.

Four new species of crocodilian are identified from the late Oligocene White Hunter Site, Riversleigh, northwestern Queensland, one of which is also found in other System A sites at Riversleigh. All four species are assigned to known genera and some revision of two generic diagnoses is required. Two different forms of posterior cranium are also identified from White Hunter Site and retained in open nomenclature. Palaeoecological significance of four crocodilians in a single site are interpreted as a sympatric assemblage because they have different head shapes. However, the diversity in these crocodilians could also suggest a thanatocenosis involving taxa from different hydrodynamic regimes with differing degrees of forest canopy cover. □ Riversleigh, Baru, Quinkana, Mekosuchus, Oligocene.

Paul Michael Arthur Willis, Quinkana Pty Ltd, 3 Wanda Cres., Berowra Hts, NSW, 2082; received 4 November 1996.

The fossil assemblage from White Hunter Site at Riversleigh, NW Queensland contains skull fragments and postcranial material of crocodilians and other vertebrates. The fragments represent at least 4 crocodilian species. Three different maxillae are assigned to new species of known genera. Of 4 mandibles identified 3 are assigned to 3 of the species identified by maxillae; the fourth belongs to a species better known from Riversleigh's D, Sticky Beak and Pancake Sites (Willis et al., 1990). Cranial material is described but not assigned to any of the 4 new species.

Mekosuchus Balouet & Buffetaut, 1987 and *Baru* Willis et al., 1990 were previously monotypic and their generic diagnoses require revision in the light of new species assigned below. *Quinkana* was revised by Willis & Mackness (1996) and their expanded generic diagnosis (based on Molnar, 1981) encompasses the new species described here.

Mekosuchus was known from Recent cave deposits in New Caledonia. It has a unique autapomorphy: the maxilla participating in the orbit. *M. whitehunterensis* sp. nov. is the first pre-Pleistocene record of this genus.

Quinkana has 3 species: *Q. fortirostrum* Molnar, 1981 from E Queensland; *Q. timara* Megirian, 1994 is more slender-snouted from late middle Miocene of Bullock Creek, NT; and *Q. babarra* Willis & Mackness, 1996 is from early Pliocene at Allingham Creek, Queensland. *Quinkana* is distinguished by a suite of ziphodont features and is unique among mekosuchines (*sensu* Willis et al., 1993) in being a broad-snouted ziphodont. *Quinkana meboldi* sp. nov. is

the third pre-Pliocene record after *Q. timara* and a species from the late Miocene Ongeva Local Fauna, Alcoota, NT (Murray & Megirian, 1992; Murray et al., 1993; Megirian, 1993).

Baru darrowi (Willis et al., 1990) was described from middle Miocene of Bullock Creek, NT and Site D, Riversleigh. Two species of *Baru* (Willis et al., 1990) are recognised from White Hunter Site. One species is particularly small for the genus and the other species is based on material from a number of Riversleigh's System A sites (*sensu* Archer et al., 1989), including White Hunter Site. Some of the material assigned here to the second species of *Baru* was previously assigned to *B. darrowi*. *Baru* species are broad, moderately deep-snouted mekosuchines with moderately compressed teeth and a distinctive ridge on the posterior of the maxilla and the jugal.

Mekosuchus, *Quinkana* and *Baru* can all be shown to be mekosuchines. A more detailed phylogenetic analysis of these three genera forms part of a more comprehensive investigation of the phylogeny of mekosuchines (Salisbury & Willis, 1996).

The ecological implications of four crocodilians in the same deposit invites an investigation of the possible structure of crocodilian faunas. There would appear to be no ecological conflict between the sympatric existence of all four species because their different morphologies suggest the exploitation of different habitats. This is consistent with modern analogies such as some parts of the Amazon River Basin and with other fossil deposits such as Messel and Geisaltal in Germany, the Bridger Basin in the U.S.A. and the La

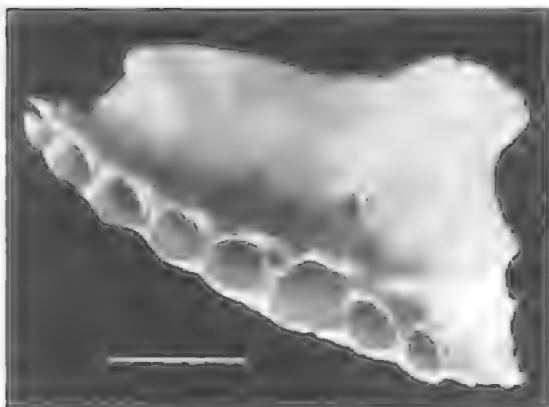


FIG. 1. *Mekosuchus whitehunterensis* n.sp., QMF31051, holotype, right maxilla, ventral view. Scale = 5mm.

Venta fauna in Colombia. Alternatively, the different crocodilians in White Hunter Site may be from different habitats and have been collected together in a thanatocenosis.

This publication was the content of a seminar presented at the Conference on Australia Vertebrate Evolution, Palaeontology and Evolution (CAVEPS) in Alice Springs, March, 1991 and published as an abstract (Willis, 1992).

Mekosuchus Balouet & Buffetaut, 1987

TYPE SPECIES. *Mekosuchus inexpectatus* Balouet & Buffetaut, 1987.

DIAGNOSIS (translated from French). Eusuchians with choanae relatively little displaced posteriad; wings of pterygoids strongly developed posteriorly; skull deck very broad; maxilla participating in lower border of the orbit; external nares opening to the side and the front (anterolaterally); nasals not reaching external nares; palatines very narrow in their posterior part; quadratojugal lacking a spine; snout short and

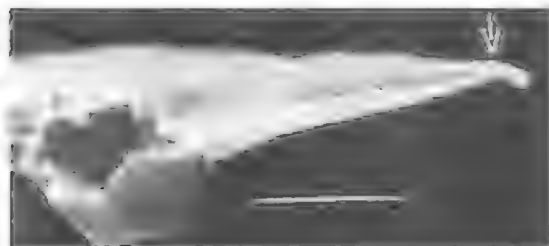


FIG. 2. *Mekosuchus whitehunterensis*, QMF31051, holotype, right maxilla. Dorsal view with white arrow showing portion of the maxilla that participates in the orbit. Scale = 2mm.

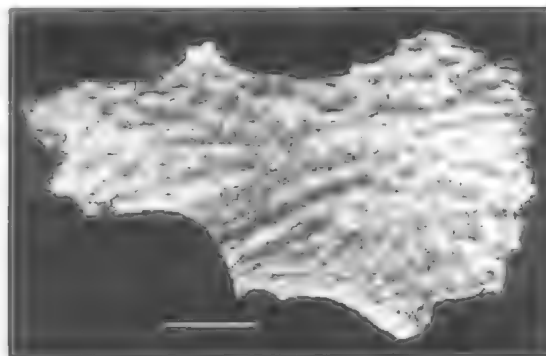


FIG. 3. *Mekosuchus whitehunterensis*, QMF31052, partial frontal, dorsal view. Scale = 5mm.

deep; splenial does not participate in the mandibular symphysis; posterior crushing teeth; 13 mandibular teeth; lower teeth occlude medial to upper series; vertebrae procoelous with strong neural spines in the cervical region; limb bones showing strong muscle insertions; presence of dorsal scutes.

My diagnosis includes the following features (apomorphies indicated by 'a') are: 1, (a) maxilla participating in lower border of the orbit. 2, snout short and deep. 3, (a) no conspicuous gap between the sixth and seventh maxillary alveoli. 4, high, narrow alveolar process. 5, symphyseal region very shallow dorsoventrally. 6, splenial anterior to the level of the seventh dentary alveolus. 7, external mandibular fenestrae strongly reduced. 8, (a) out-turned flange on the angular and surangular.

The type species diagnosis is: palatal fenestrae reaching anteriorly to the level of the sixth maxillary alveoli; posterior teeth of rounded, crushing form; symphysis reaching posteriorly to the level of the seventh dentary alveoli.

Some features of the original diagnosis are synapomorphies of wider groups and others are of uncertain value so they are not employed herein.

The character 'nasals not reaching external nares' is equivocal on available material so is not employed pending more complete material.

Mekosuchus whitehunterensis sp. nov. (Figs 1-5)

MATERIAL. Holotype. QMF31051, right maxilla (Figs 1, 2). Paratypes QMF31052, partial frontal; QMF31053, almost complete mandible; QMF31054 and QMF31055, anterior portions of dentaries. All from late Oligocene White Hunter Site, Riversleigh.

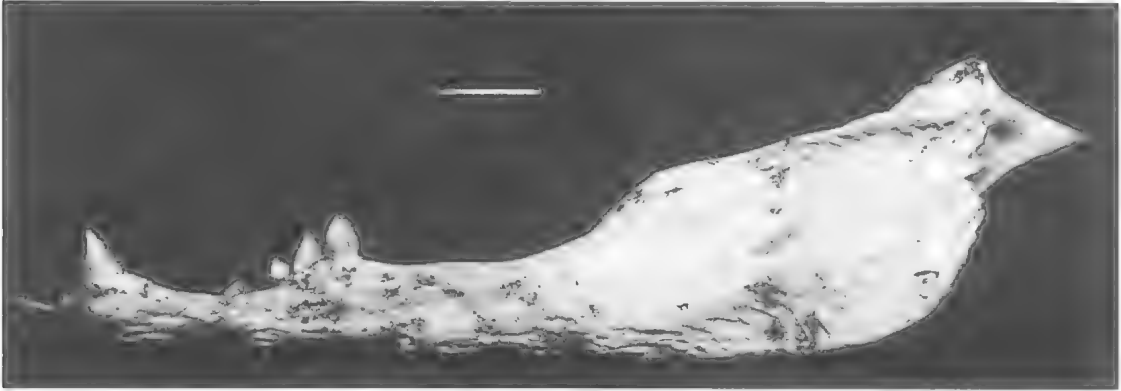


FIG. 4. *Mekosuchus whitehunterensis*, QMF31053, left mandible, lateral view. Scale = 1cm.

DIAGNOSIS. Longitudinal sulcus below the orbit; palatal fenestrae reaching anteriorly to the level of the seventh maxillary alveoli; posterior teeth compressed and blade-like; and symphysis extending posteriorly to the level of the sixth dentary alveoli.

ETYMOLOGY. From White Hunter Site.

DESCRIPTION. Maxilla broad, deep-snouted, with moderately high, narrow alveolar process (*sensu* Molnar, 1981). Lateral wall steeply in-

clined to the palate, with longitudinal sulcus ventral to the orbit. Small portion of the maxilla participating in the orbit, separating lacrimal from jugal. (Full extent to which the maxilla participated in the orbit cannot be deduced because the posterior portion is missing in this specimen.). Alveoli ovate, slightly compressed laterally, close to each other so excluding the lower series from resting between them; fifth alveolus largest; first and seventh alveoli small-

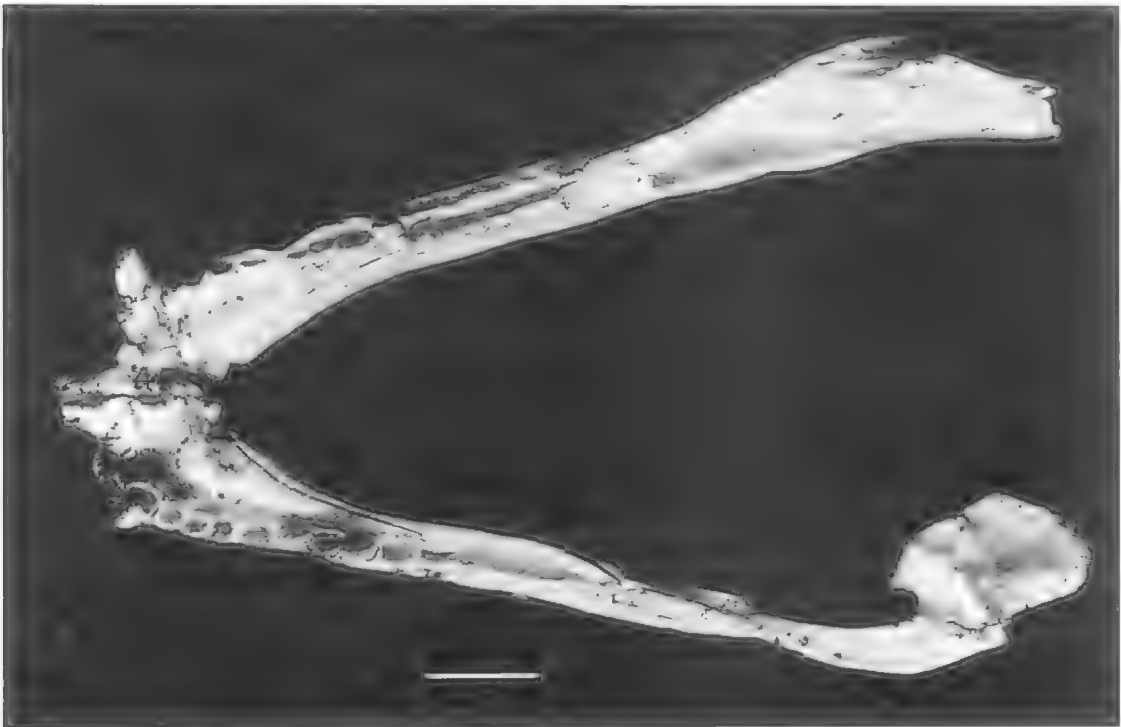


FIG. 5. *Mekosuchus whitehunterensis*, QMF31053, left mandible, dorsal view. Scale = 1cm.

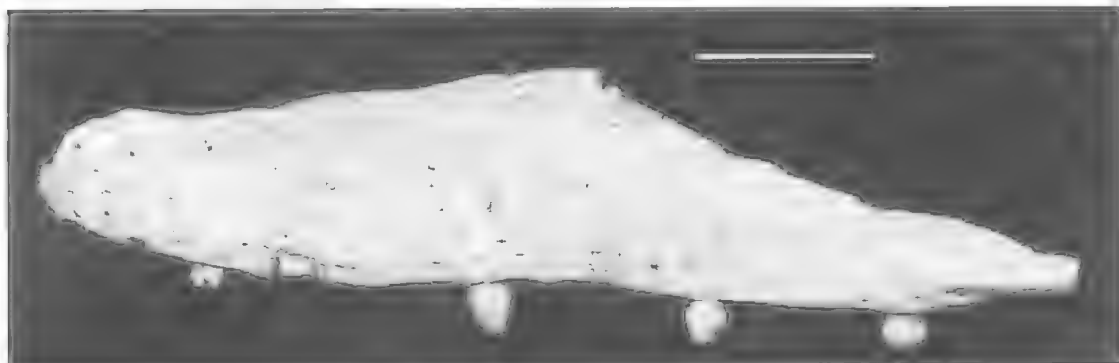


FIG. 6. *Quinkana meboldi* n. sp., QMF31056, holotype, left maxilla, lateral view. Scale = 1 cm.

est, almost equal in size. Only two pits for reception of dentary teeth medial to the upper alveoli, between the sixth and seventh alveoli, and a disproportionately large pit posterior and medial to the seventh alveolus. Palatal fenestra reaching level of the seventh alveolus.

Frontal. Closely resembles frontals of *M. inexpectatus*, very wide between the orbits; orbit margins raised, giving a concave transverse section to the dorsal surface. *crania cristae frontalis* shallow, close together leaving a wide, thin shelf between them and the orbit margins.

Mandible and dentary fragments. Pseudoheterodont with an undulating tooth row; tooth row shorter with respect to the whole mandible than in other crocodiles. Posteriorly, dentary strongly compressed laterally and deep dorsoventrally. Dentary thick around the base of each alveolus; buttressing variable in proportion to size of alveolus, not strongly developed. Slight ridge defining a groove lateral to the 12th through to the 16th alveoli probably received posterior maxillary

teeth. Splenial extending anteriorly to 7th alveolus; symphysis extending to 6th. Low ridge on the external surface of both dentaries running from below the 8th dentary alveolus onto the angular, probably strengthened the dentary. Teeth 16, with unserrated anterior and posterior carinae, becoming laterally compressed posteriorly so that posterior teeth are blade-like.

QMF31053 with large, out-turned flange on the posterior and ventral margins of angular and out-turned flange on the dorsal margin of the external surface of the surangular; flanges joining at the posterior margin of the mandible, marking boundary between the sculptured surfaces and the smoother surfaces for muscle attachment.

Articular broad, expanded medially; articular portion of retroarticular process shallowly concave. Retroarticular process short and steeply inclined. Medial side of condylar surface reduced, strongly buttressed ventrally. External mandibular fenestra reduced, almost closed. Sculpture of indistinct scarring on the external

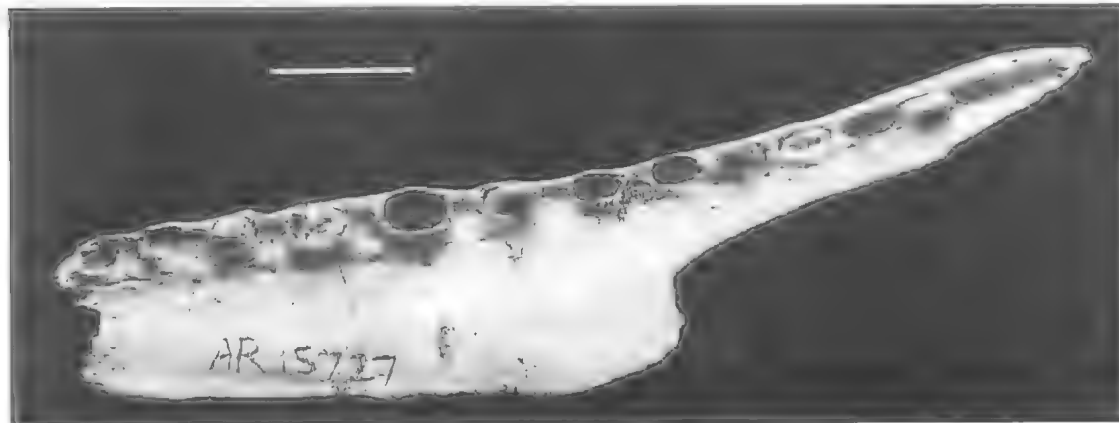


FIG. 7. *Quinkana meboldi* n. sp., QMF31056, holotype, left maxilla, ventral view. Scale = 1 cm.

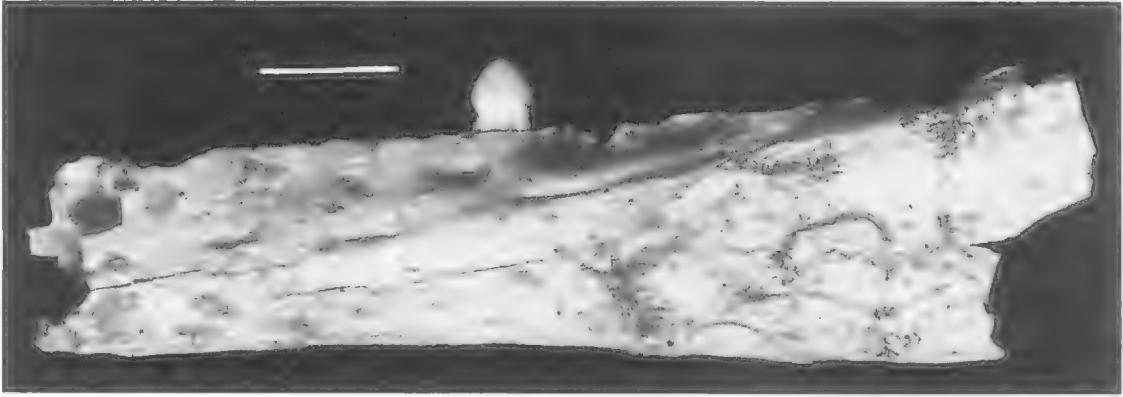


FIG. 8. Left dentary of *Quinkana meboldi* (QMF31059). Lateral view, scale = 1cm.

surfaces of the dentary and a well-developed mosaic of pits on the angular and surangular.

DISCUSSION. This mandible is very derived and shows distinct similarities to *M. inexpectatus*. Both are distinguished by: external fenestra reduced or closed; anterior edge of surangular forming distinct step dorsal to the dentary; angular and surangular flange; posterior portion proportionally short and deep; symphysis very shallow; similar sculpture. Maxillae of *M. inexpectatus* and *M. whitehunterensis* exhibit the apomorphic condition of contacting the orbit. Thus, it is most parsimonious to associate the derived mandible and maxilla from White Hunter Site, both of which most closely resemble *M. inexpectatus*. The association of mandibles and maxillae of *M. inexpectatus* is not in doubt (Balouet pers. comm.).

***Quinkana* Molnar, 1981**

TYPE SPECIES. *Quinkana fortirostrum* Molnar, 1981

DIAGNOSIS. See Willis & Mackness (1996).

***Quinkana meboldi* sp. nov.**
(Figs 6-9)

MATERIAL. Holotype QMF31056, left maxilla (Figs 6, 7). Paratypes QMF31057, almost complete left maxilla; QMF31058, right maxillary fragment; QMF31059, dentary fragment. All from late Oligocene White Hunter Site, Riversleigh.

DIAGNOSIS. Small to moderate-sized, with 14 maxillary alveoli; palatal fenestra extending anteriorly to the level of the 8th maxillary alveolus; teeth partially interlock; snout narrower than in *Q. fortirostrum*; mild festooning; carinae of teeth without serrations.

ETYMOLOGY. For Ulrich Mebold, Max Plank Institut für Radioastronomie.

DESCRIPTION. Maxilla. Teeth 14, compressed and blade-like with anterior and posterior carinae. Alveoli compressed to varying degrees; anterior 6 teeth directed slightly posteriorly.

Alveolar ridge low, mildly undulating, uninterrupted laterally but medial side interrupted by pits for the reception of dentary teeth. Palatal fenestra extending anteriorly to the 8th alveolus. Midline palatal suture straight to the level of the 7th alveolus, then diverting laterally to accommodate a short, pointed anterior palatal process.

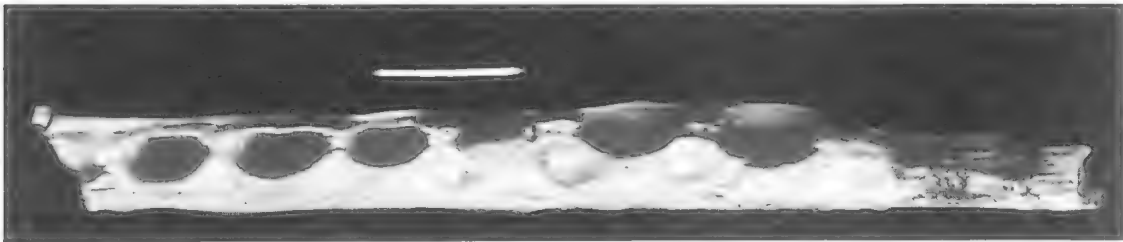


FIG. 9. *Quinkana meboldi*, QMF31059, left dentary, dorsal view. Scale = 1cm.

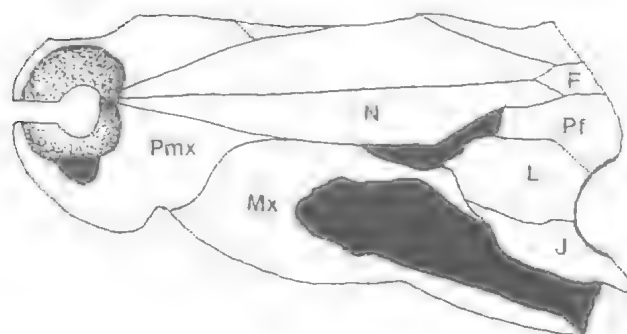
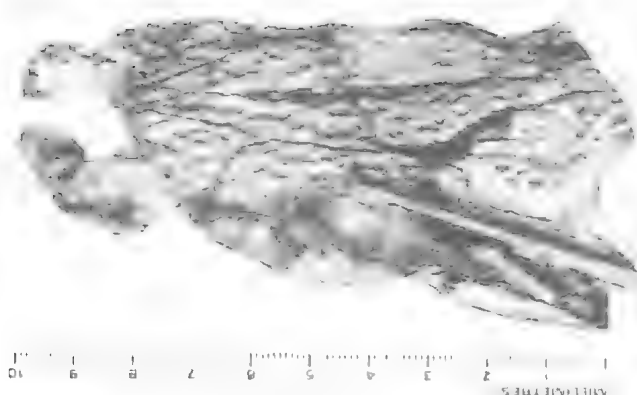


FIG. 10. *Baru huberi*, QMF31060, holotype, snout, dorsal view, with line interpretation. F=frontal; J=jugal; L=lacrimal; Mx=maxilla; N=nasal; Pf=prefrontal; Pmx=premaxilla. Scale in cm.

Dorsal surface steep-sided, indicating a deep, moderately broad snout. Preorbital or lacrimal ridge giving the snout a trapezoidal cross section anterior to the orbits. Margins contacting nasals straight. Sculpture of distinct pits anteriorly, degenerating to pitted scars posteriorly.

Alveoli with a sharply defined groove running medial to the alveoli. This appears to have been derived from the line of foramina normally found in other crocodylians in a homologous position.

DISCUSSION. The lateral compression of both the dentary and the dentition as well as the lack of festooning indicates that the dentary fragment (QMF31059) belongs to *Q. meboldi*. The single tooth is identical to the posterior teeth of QMF31056. This dentary form differs from *M. whitehunterensis* in which the posterior-most alveoli are interconnected. It also differs from dentaries attributed to *Baru* which lacks strongly

compressed alveoli and does not have a laterally compressed mandibular body.

Baru Willis, Murray & Megirian, 1990

TYPE SPECIES. *Baru darrowi* Willis et al., 1990.

DIAGNOSIS. Broad, moderately deep snout; reduction of the second premaxillary tooth during growth sometimes resulting in four premaxillary teeth in adults; premaxillary and anterior six maxillary teeth directed posteriorly; tooth crowns moderately compressed laterally; tooth crown and socket dimensions highly differentiated along both upper and lower tooth rows with correspondingly wide, deep alveolar processes; conspicuous maxillary reception pits corresponding to dentary tooth crowns situated medial to the upper tooth row; anterior margins of the palatal fenestrae extending to the level of the seventh maxillary tooth; anterior palatine process absent; splenial terminates anteriorly at the level of the seventh dentary tooth and does not enter

symphysis; external nares terminal and broadly 'apple'-shaped; distinctive bony crest arches posteriorly from the maxillae and jugals, extending to the quadratojugals.

REMARKS. The 2 new species are most closely related to Miocene *B. darrowi* from the NT (Willis et al., 1990). Some of the material attributed here to *B. wickeni* sp. nov. was previously referred to *B. darrowi*. 'Internal nares with raised rim' was included in the original diagnosis of *Baru* but its status is now uncertain.

Baru darrowi Willis, Murray & Megirian, 1990

DIAGNOSIS. Snout broad, deep; rounded premaxillae; 13 maxillary teeth; nasals excluded from external nares; anterior termination of nasal

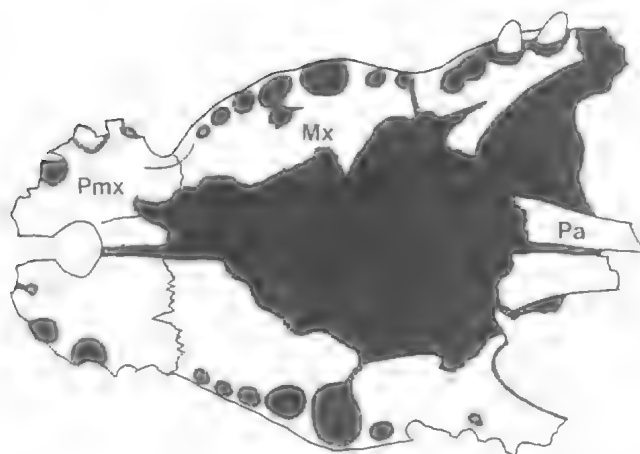
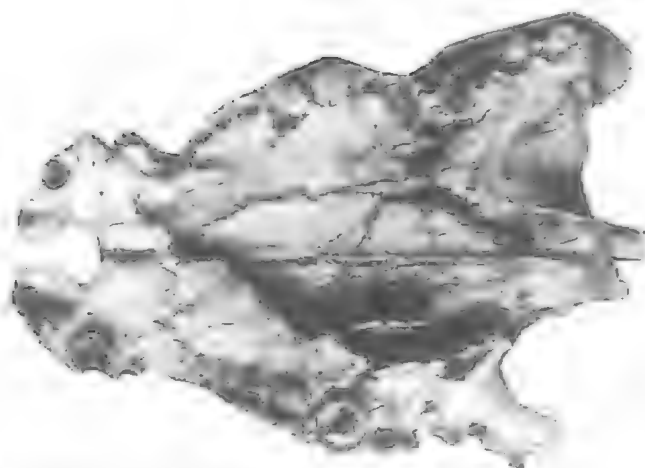


FIG. 11. *Baru huberi*, QMF31060, holotype, snout, ventral view, with line interpretation. Mx=maxilla; Pa=palatine; Pmx=premaxilla. Scale in cm.

is a short, broad wedge; serrated carinae; mandibular symphysis extends posteriorly to between the sixth and seventh dentary teeth.

***Baru huberi* sp. nov.**
(Figs 10, 11)

HOLOTYPE, QMF31060, fragmentary snout (Figs 10, 11). **PARATYPES** QMF31061, right premaxilla and anterior portion of right maxilla; QMF31062, relatively complete premaxilla; QMF31063, partial maxilla; QMF31064, maxillary fragment; QMF31065, maxil-

lary fragment; QMF31066, maxillary fragment; QMF31067, dentary; QMF31068, dentary; and QMF31069, pair of dentaries with splenial fragments. All from late Oligocene White Hunter Site, Riversleigh.

DIAGNOSIS. Snout broad, not as deep as in other species; rounded premaxillae; 14 maxillary teeth; nasals contact external nares; lateral border of the nasals without angulation at the maxilla-premaxilla boundary; non-serrated carinae; mandibular symphysis extending posteriorly to the 5th dentary teeth.

ETYMOLOGY. For Professor Huber, Rektor of the Friedrich Wilhelms Universität, Bonn

DESCRIPTION. Skull anterior to orbit. Snout low, broad; premaxillary alveoli circular, 4th largest, 5 in juvenile, with 2nd alveolus reduced and almost lost, 4 in adult (2nd lost). Incisive foramen broad, tear-shaped; external nares apple-shaped, with a short anterior process of the premaxilla and nasals on its posterior margin. Deep reception pit for the first dentary tooth not reaching dorsal surface. Fourth dentary tooth reception notch prominent, with a secondary pit medial to it on the palate. Premaxillary-maxillary suture relatively straight, with a slight posterior convexity. Maxillary alveoli 14, arranged in a typically crocodyline enlargement sequence with the 5th largest, laterally compressed particu-

larly the posterior-most 5. Low alveolar process on the anterior 6 maxillary alveoli. Dentary tooth reception pits 5, well-developed, medial to the upper series, between 6th-11th alveoli. Anterior teeth moderately robust, ovate in cross section. Posterior teeth with low, rounded crowns. All teeth with distinct anterior and posterior carinae. Palatal fenestra extending anteriorly to between the 7th and 8th maxillary teeth; straight suture with the palatine forming a short palatal process reaching anteriorly to 6th alveolus. Broad shelf

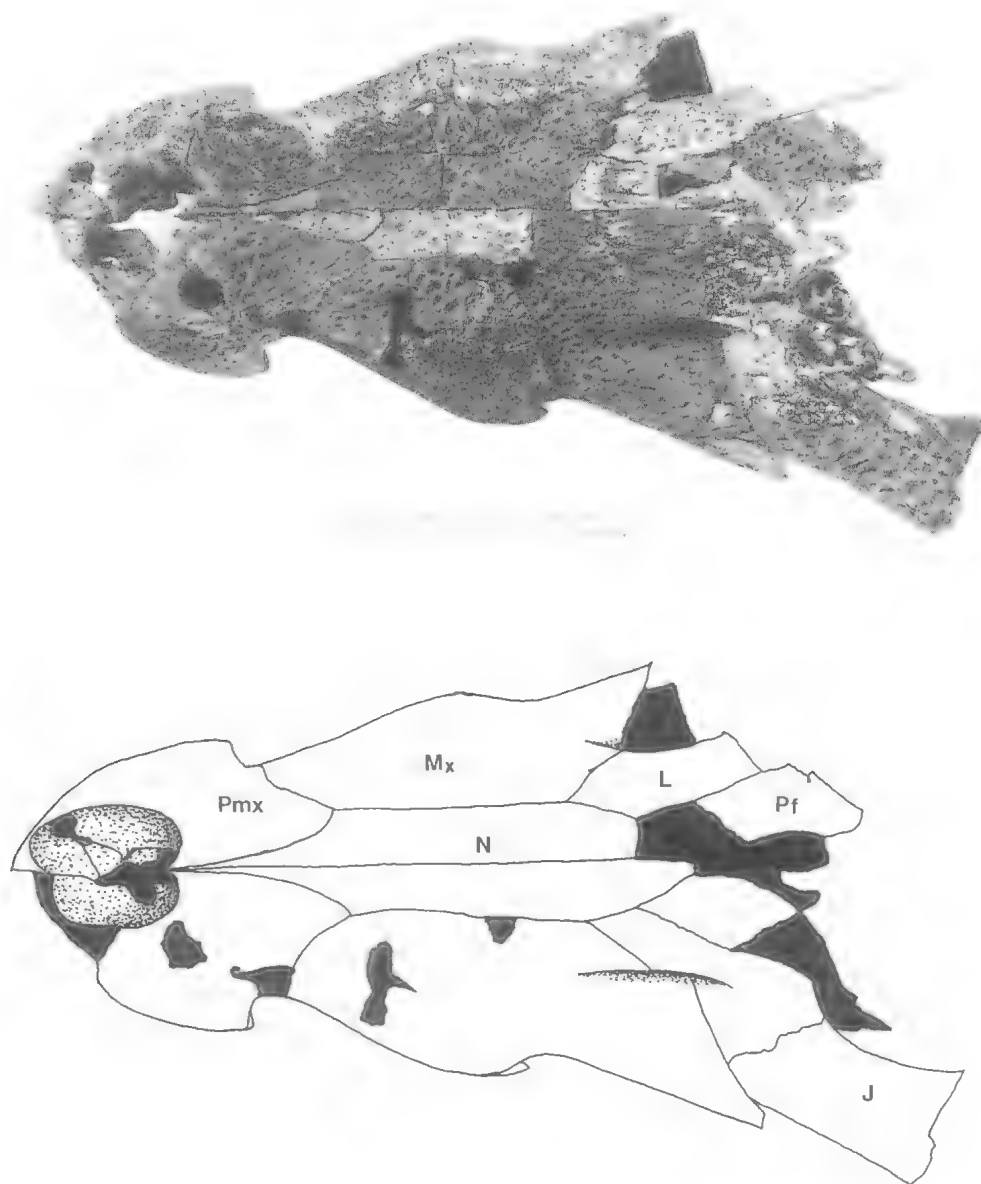


FIG. 12. *Baru wickeni*, QMF 16822, holotype, dorsal view, snout, with line interpretation. F=frontal; J=jugal; L=lacrimal; Mx=maxilla; N=nasal; Pf=prefrontal; Pmx=premaxilla. Scale in cm.

between palatal fenestra and posterior alveoli, rounded dorsally into the palatal fenestra and on to the internal surfaces of the maxilla. Sharp-crested ridge on the external surface of the maxilla at the line of the palate, starting above 10th alveolus, running off the posterior border of the maxilla.

Nasals broad, contacting the external nares, gradually widening to the lacrimal-maxilla-nasal triple junction, then tapering more sharply. Short, pointed anterior process of the frontals dividing the posterior extremities of the nasals. Lacrimals with low, rounded canthi rostrales, about twice the size of the prefrontals.

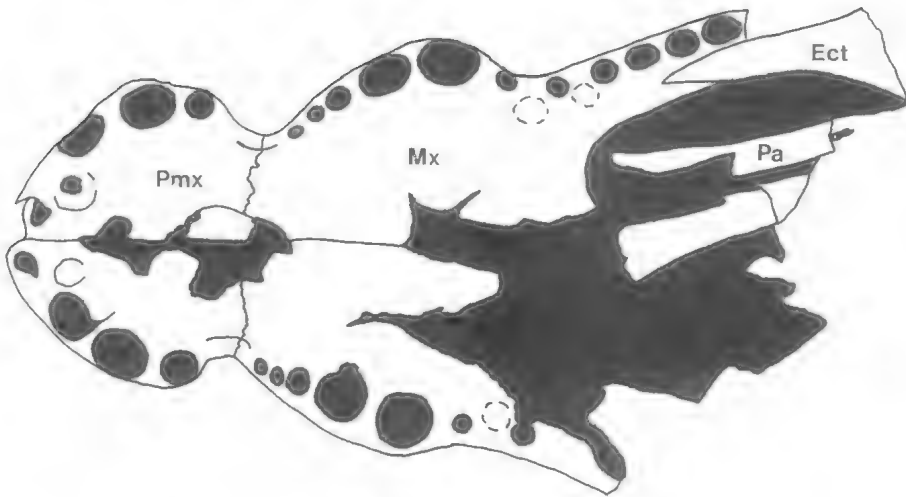


FIG. 13. *Baru wickeni*, QMF16822, holotype, snout, ventral view, with line interpretation. Ect=ectopterygoid; Mx=maxilla; Pa=palatine; Pmx=premaxilla. Scale in cm.

Dentary fragments. Dentary pseudoheterodont, with an undulating tooth row. Symphyseal region deeper and larger than in *Mekosuchus*. Dentary built up around the base of each alveolus, with this buttressing variable in proportion to size of the alveolus and not strongly developed. Slightly raised area on the dorsal surface medial to the 4th and 5th alveoli. Dorsal margin of dentary be-

tween and lateral to the 2nd and 3rd alveoli and between and lateral to the 7th, 8th and 9th alveoli with indentations for reception of teeth in the upper series, indicating that the upper series occluded lateral to the lower series. Splenial extending anteriorly to the 7th alveolus; symphysis extending to 5th alveolus. Sculpture of indistinct

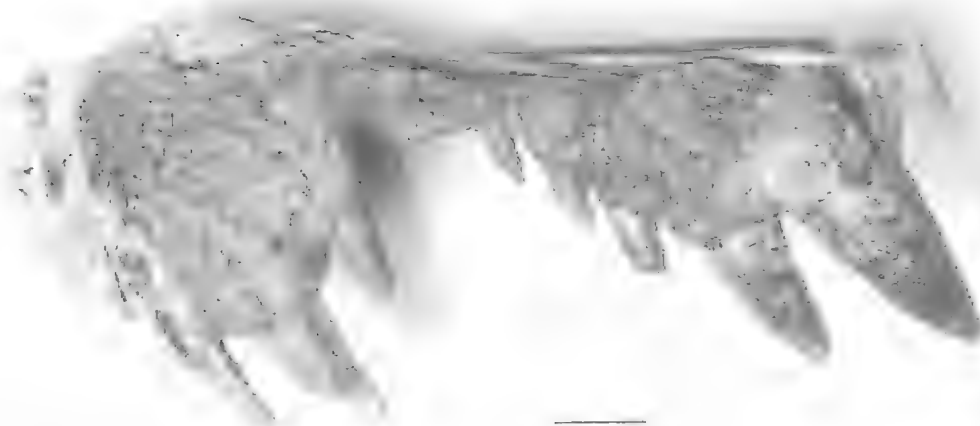


FIG. 14. *Baruwickenia*, QMF16822, holotype, partial left maxilla and premaxilla, lateral view. Scale = 2cm.

scarring on the ventral surfaces of the dentary merging to well developed pitting dorsally.

DISCUSSION. This mandible is assigned to *B. huberi* because it is the only unassigned mandible of appropriate proportions and size range from White Hunter Site. QMF31068 is an almost exact fit for QMF31060. The other 3 mandibular forms from White Hunter Site can be shown to belong to other taxa.

***Baru wickeni* sp. nov.**
(Figs 12-17)

MATERIAL. Holotype, QMF16822 (Figs 12-14) associated posterior cervical and lumbar vertebrae and a calcaneum. Paratypes QMF31070, anterior portions of mandibles; NTM P8738-1, posterior right skull fragment and associated right anterior dentary fragment; NTM P8681-14, left mandible lacking the articular and adjacent angular and surangular posterior to the lateral foramen and a small portion of the dentary at the level of the third tooth; NTM P8738-1, right jugal, pterygoid, ectopterygoid and posterior maxilla and an associated dentary fragment; QMF16823, jugal fragment; QMF16824, premaxillary fragments; QMF16825, right dentary; QMF16826, right dentary. All from Oligocene (System A) Site D, Riversleigh. QMF31071 and QMF31072, posterior portions of large mandibles and QMF31073, anterior dentary fragment. All from late Oligocene White Hunter Site, Riversleigh. SAMP27866, right premaxilla from late Oligocene Pancake Site, Riversleigh. QMF31074, right maxillary fragment and fragment of skull roof from late Oligocene Sticky Beak Site, Riversleigh.

ETYMOLOGY. For Tony Wicken, University of NSW, for supporting the Riversleigh Research Project.

DIAGNOSIS. Snout narrower than *B. huberi* or *B. darrowi*; deep; anteriorly pointed premaxillae; 13 maxillary teeth; nasals entering external nares; anterior termination of nasals long and thin, strongly constricted by premaxillae; non-serrated carinae; mandibular symphysis extending posteriorly to 6th or 7th dentary teeth.

DESCRIPTION. Skull material. Snout narrower than *B. darrowi* or *B. huberi*, similar in depth to *B. darrowi*. Premaxilla pointed anteriorly rather than rounded as in the other 2 species. Teeth similar to *B. darrowi*, lacking serrated carinae. Premaxillary alveoli in adults 4, in juveniles 5, with 2nd alveolus lost during growth. Maxillae with short posterior process medially invading lacrimal (not present in *B. darrowi* and unknown in *B. huberi*). Maxillary alveoli 13; palatal fenestra extending anteriorly to the level of 7th maxillary alveolus. Nasals entering premaxillae unlike *B. darrowi* but similarly to *B. huberi*. Anterior nasals distinctive in *B. wickeni*, being thin slivers strongly constricted between the premaxillae. Lacrimal with distinct, rounded *canthus rostralis*, extending for a short distance onto the maxilla. Jugal with well-defined, arched ridge on the exterior surface.

Mandibles. Alveoli 15, subcircular except for the 4 slightly laterally compressed most posterior. Alveoli 3rd-6th on an alveolar process most strongly developed around the 4th alveolus. No

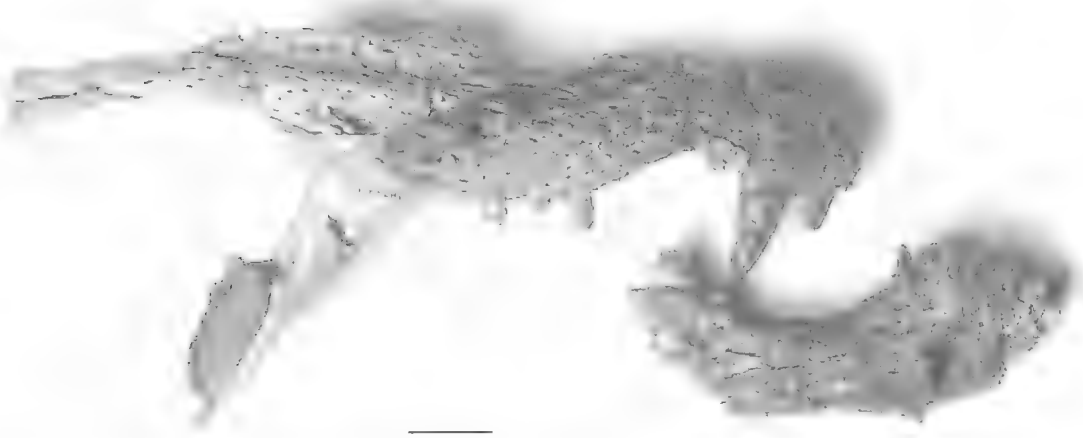


FIG. 15. *Baruwickeni*, NTM P8738-1, portions of the right side of the skull with associated dentary fragment, lateral view. Scale = 2cm.

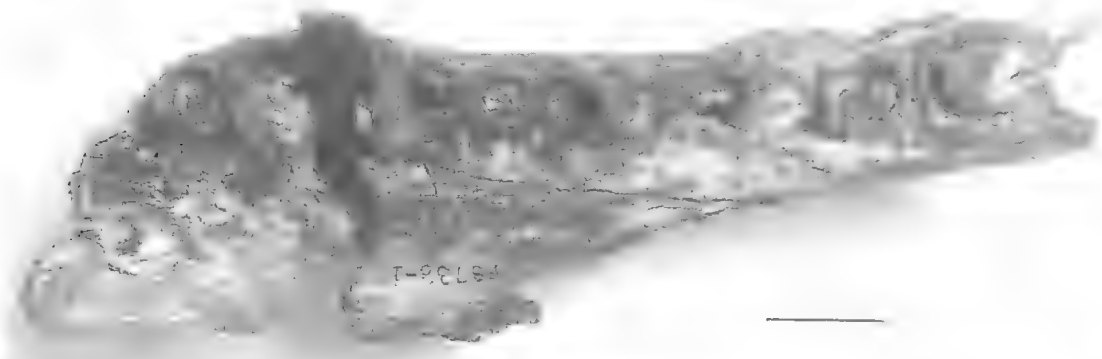


FIG. 16. *Baruwickeni*, NTM P8738-1, dentary fragment, dorsal view. Scale = 2cm.

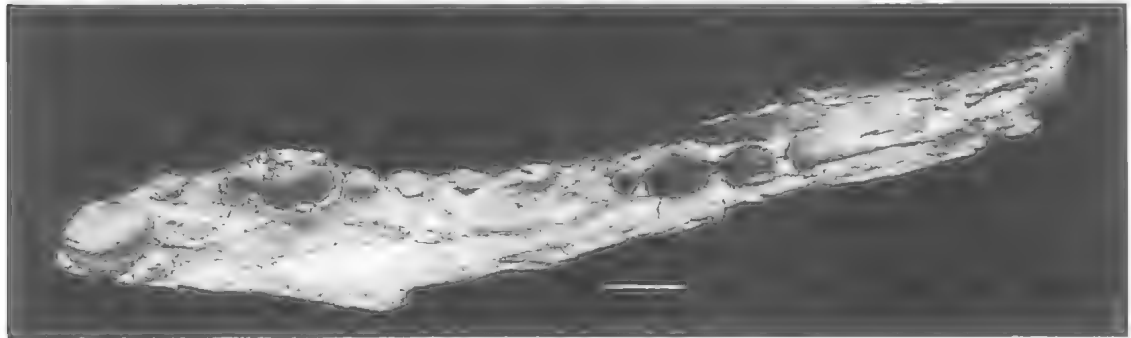


FIG. 17. *Baruwickeni*, QMF31070, dentary, dorsal view. Scale = 2cm.

reception pits for teeth from the upper series but spacings and a lateral sulcus between 2nd and 3rd alveoli, 7th and 8th alveoli and between the 8th and 9th alveoli. Symphyseal region narrow. Sym-

physis extending posteriorly to 6th alveolus; splenial reaching anteriorly to 7th.

External mandibular fenestrae ovate, of moderate size and inclined posteriorly. Surangular narrow dorsoventrally, inclined posteriorly with

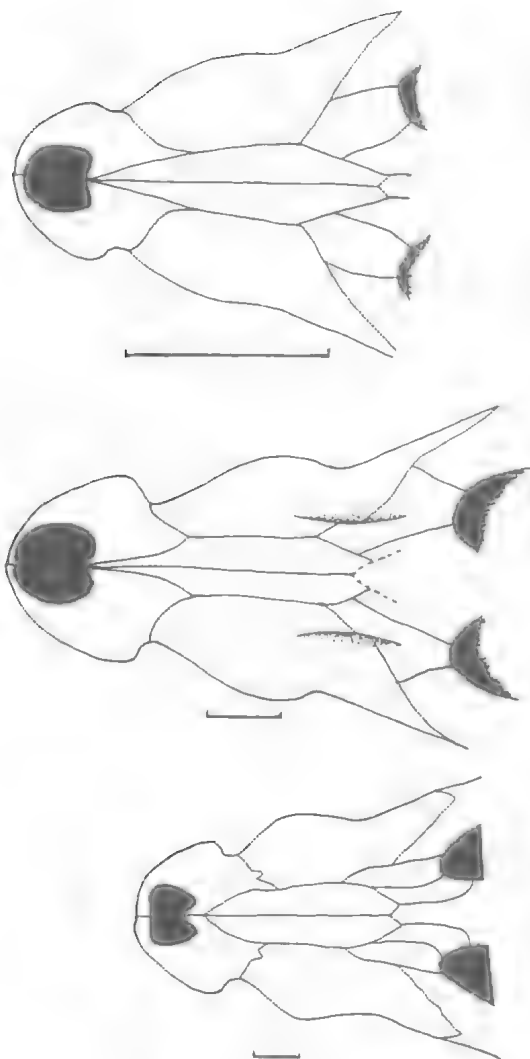


FIG. 18. Dorsal views of reconstructed snouts of *Baru huberi* (top), *B. wickeni* (middle) and *B. darrowi* (bottom) showing differences in sutural relations, particularly in the nasal-premaxillae sutures, and general proportions. *Baru huberi* based on QMF31060 (holotype), *B. wickeni* based on QMF16822 (holotype) and *B. darrowi* based on NTMP8695-8 (holotype). Scale = 5cm.

dorsal margin not parallel to the dentary. Angular slender, inclined. Smooth region for attachment of the posterior pterygoideus musculature sharply demarcated from the heavily sculptured areas of the angular and surangular by a low ridge. Articular and retroarticular process short, broad and steeply inclined.

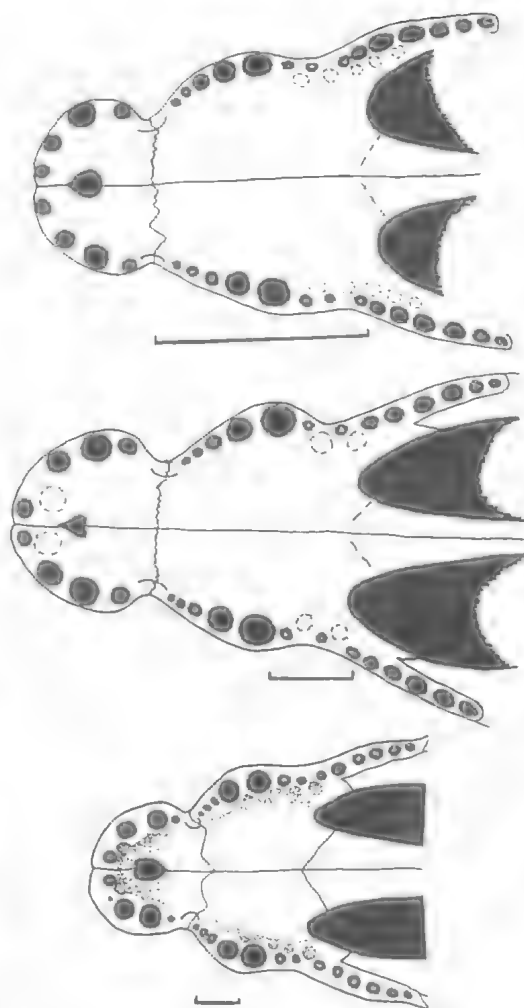


FIG. 19. Ventral views of reconstructed snouts of *Baru huberi* (top), *B. wickeni* (middle) and *B. darrowi* (bottom) showing differences in general proportions. *Baru huberi* based on QMF31060 (holotype), *B. wickeni* based on QMF16822 (holotype) and *B. darrowi* based on NTMP8695-8 (holotype). Scale = 5cm.

DISCUSSION. This new species is based primarily on material from Site D.

In describing *B. darrowi*, Willis et al. (1990) recognised that specimens from Bullock Creek differed from specimens from Riversleigh. However, at that stage there was insufficient material to separate 2 species. Since then a large portion of a snout from Riversleigh (part of QMF16822) a fragment of which was in the original description of *B. darrowi* has been rediscovered and

prepared. This and other new material allows the material from Riversleigh to be allocated to a third species of *Baru* (Figs 18, 19).

TWO CRANIAL FORMS

White Hunter Site has produced several posteriors of crocodilian skulls and skull decks representing 2 similar forms. No specimen duplicates portions of other specimens so although the cranial forms almost certainly pertain to 2 of the taxa described above, they cannot be assigned.

WHITE HUNTER CRANIAL FORM 1 (Figs 20-22)

MATERIAL. QMF31075, 31076 posterior of skulls; QMF31077, skull fragment; QMF31078, isolated parietal.

DIAGNOSIS. Supratemporal fenestrae tear-shaped with point directed anterolaterally and with posterior shelf formed by the squamosal; prominent expression of supraoccipital on skull deck; postorbital bar slender and round in section; postorbital-frontal suture twice the length of postorbital-parietal suture; foramen magnum wider than occipital condyle; width of supratemporal fenestrae greater than width of postorbital; sculpture of more or less regular pits closely spaced.

DESCRIPTION. Wide across the skull deck, high with the quadrate tucked under the squamosals. Supraoccipital prominent on the dorsal surface, forming a broad triangle almost excluding parietals from posterior margin of skull deck. Supratemporal fenestrae with an anterior point, teardrop-shaped, with much of the posterior and medial portions closed by a floor formed by the squamosal and parietals inside the supratemporal fenestrae. Posterior face of the skull with pronounced concavities on exoccipitals and squamosals for attachment of mandibular depressor muscles. Paroccipital process encroaching ventrally onto the quadrate. Foramen magnum subtriangular, wider than the occipital condyle. Basioccipital with pronounced keel ventral to the occipital condyle. Quadrates steeply inclined. Pterygoids forming large portion of the posterior margin of the palatal fenestrae; internal nares, although not preserved, must have been well to-



FIG. 20. Cranial form 1, QMF31075, posterior portion of skull, dorsal view. Scale = 1cm.

ward the posterior of the pterygoids. Otic meatus and foramina for the trigeminal nerve proportionally large. Laterosphenoids with a pronounced longitudinal crest medially on the ventral surface. Sculpture on the skull deck distinctive, deep and well-defined pits separated by equally distinct, uniform walls. Pits close spaced.

WHITE HUNTER CRANIAL FORM 2

MATERIAL. QMF31079, anterior fragment of skull deck; QMF31080, right postorbital.

DIAGNOSIS. Small supratemporal fenestrae laterally compressed, shallowly floored by squamosals; postorbital bars inset from skull deck margin, robust and triangular in section; postorbital-frontal suture equal in length to postorbital-parietal suture; width of postorbital greater than width of supratemporal fenestrae; sculpture of irregular shaped pits with irregular distribution.

DESCRIPTION. WH 2 is described where it differs from WH 1.

Supratemporal fenestrae narrower; squamosal flooring making supratemporal fenestrae shallower posteriorly. Sculpture pits on WH 2 are small and irregular, separated by thick, irregular walls. Sculptured skull deck overhanging postorbital bar on WH 2 but in WH 1 postorbital bar

marginal. Postorbital bar moderately robust, with triangular cross section. Postorbital very large compared to the supratemporal fenestrae. Triple junction between the postorbital, frontal and parietal distant from margins of supratemporal fenestrae.

DISCUSSION. The frontals associated with QMF31076 are very different from those referred to *Mekosuchus* (QMF31052) in being narrower and flat between the orbits. They are also deeper and have better defined *crania cristae frontalis* than QMF31052. Thus cranial form 1 can be confidently excluded from *Mekosuchus* (but not *Baru* or *Quinkana*).

Although there are no frontals unambiguously associated with cranial form 2, the difference in sculpture (compared with QMF31052) and the thickness of the orbit margins of the postorbital make it unlikely that this cranial form represents *Mekosuchus*.

PALAEOECOLOGY

Four crocodilians have not previously been found in a single fauna in Australia. However, compared with world faunas, this is not an unusually high diversity of crocodilians, particularly when the 4 species have differing head shapes or when the site perhaps represents a thanatocenosis collected from 2 or more habitats.

Among extant crocodilians, many species have ranges that overlap but true sympatry is not common. In parts of South America 5 or 6 crocodilian ranges overlap but rarely do 3 or more share the same habitat (Gorzula, 1987; Magnusson & Lima, 1991). The range of *Crocodylus porosus* encompasses the ranges of *C. johnstoni*, *C. novaeguineae*, *C. mindorensis*, *C. siamensis*, *Tomistoma schlegelii* and parts of the range of *C. palustris* and *Gavialis gangeticus* (Ross & Magnusson, 1989; Groombridge, 1987) but rarely do any of these species exist in true sympatry. Where *C. porosus* and *C. johnstoni* have been found in sympatry the larger *C. porosus* tends to exclude *C. johnstoni* to the margins of the habitat or

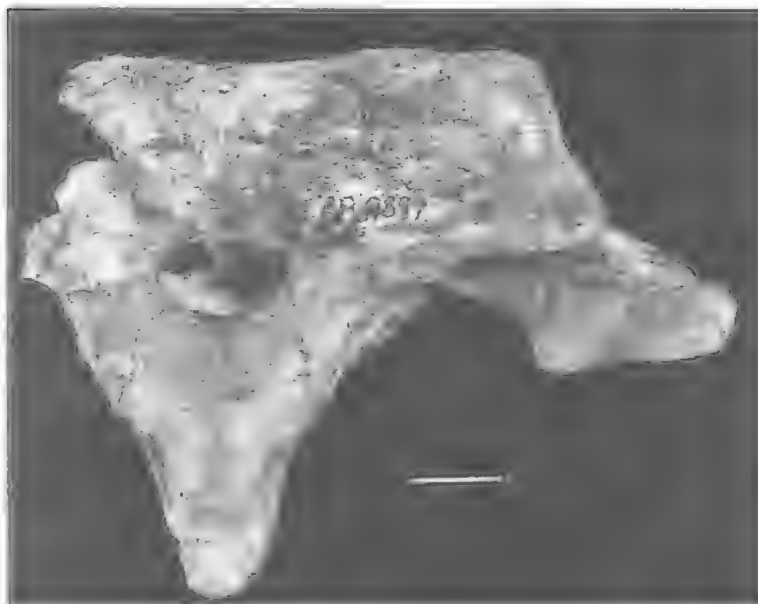


FIG. 21. Cranial form 1, QMF31075, posterior portion of skull, posterior view. Scale = 1 cm.

sympatry is restricted by the need for different nesting substrates (Webb et al., 1983).

Modern studies of crocodilians in the Amazon Basin indicate that larger watercourses are occupied by larger, generalised crocodilians such as *Melanosuchus niger* and *Caiman crocodilus* as well as *Paleosuchus palpebrosus*, while smaller watercourses in closed canopy forests are occupied only by the more derived, deep-headed *P. trigonatus* (Magnusson, 1987; Magnusson & Lima, 1991). This could suggest that the variety of crocodilian head shapes at White Hunter Site is the result of a thanatocenosis collected from 2 or more different habitats.

Theoretically, 2 crocodilians may live sympatrically when there are differences in head shape (implying exploitation of different prey) or where small, broad-snouted species can evade larger broad-snouted species by escaping to marginal habitats (Meyer, 1984). In no extant crocodilian fauna, do 2 species share the same head shape (Meyer, 1984).

The most diverse fossil crocodilian fauna is from the La Venta fauna in Colombia which consisted of 8 species (4 broad-snouted, 1 duck-bill, 2 narrow-snouted and 1 ziphodont; Langston, 1965). However, that fauna is a thanatocenosis from over 240m stratigraphically. Sympatry was not demonstrated.

The Messel fauna of Germany is more likely a biocenosis and has 6 crocodilian species including large and small broad-snouted forms, a short-snouted form and two ziphodonts. A similar assemblage has been recovered from Geisaltal (Kuhn, 1938; Haubold, 1983; Haubold & Krumbiegel, 1984).

There are two possible explanations for the diversity of crocodilians in White Hunter Site. *Baru wickeni* is a large broad-snouted form while *B. huberi* is a much smaller broad-snouted form; *Mekosuchus whitehunterensis* is a small, short-snouted form; and *Quinkana meboldi* is a ziphodont. Compared to other fossil sites around the world and to modern analogues, the White Hunter assemblage differ enough to be sympatric exploiting different niches. Alternatively, they may indicate a thanatocenosis from two or more different habitats.

Arrangements of differing ecomorphs of groups of mammals from sites at Riversleigh support the hypothesis that these faunas represent biocenoses. A complex fauna of 8 species of bandicoots, belonging to clearly defined guilds, has been recovered from Upper Site (J. Muirhead, pers. comm.). Similarly, several species of ring-tail possums of differing ecomorphs have also been found in many sites at Riversleigh (M. Archer, pers. comm.). This pattern is apparently repeated in several other groups of mammals currently being investigated. That the Riversleigh mammalian faunas repeatedly show sympatry between several closely related taxa supports the hypothesis that Riversleigh sites preserve biocenoses rather than thanatocenoses. This supports the hypothesis that the White Hunter crocodilians were also sympatric.

CONCLUSIONS

The 4 crocodilians from White Hunter Site include the first record of *Mekosuchus* outside New Caledonia and demonstrates a surprising morphological diversity suggesting significant



FIG. 22. Cranial form 1, QMF31076, posterior portion of skull, dorsal view. Scale = 1 cm.

niche separation. This is the first record of such a diverse crocodilian fauna from Australia but it is consistent with the structure and complexity of crocodilian faunas known from elsewhere. By comparison with other Riversleigh faunas the crocodilian fauna of White Hunter Site was probably typical for Oligo-Miocene Australia.

ACKNOWLEDGEMENTS

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MAYIGRIPHUS ORBUS GEN. ET SP. NOV., A MIOCENE DASYUROMORPHIAN
FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

S. WROE

Wroe, S. 1997 06 30: *Mayigriphus orbus* gen. et sp. nov., a Miocene dasyuromorphian from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41(2): 439-448. Brisbane. ISSN 0079-8835.

Mayigriphus orbus gen. et sp. nov., an enigmatic Miocene dasyuromorphian from Riversleigh, is described from dental material. The tiny *Mayigriphus orbus* shows a number of derived character-states for Dasyuromorphia and two of these derived features may signify a special relationship with *Planigale* (Dasyuridae). However, no specialised features shown by *M. orbus* are unique to dasyurids within the order and *M. orbus* also possesses derived characters shown by basal thylacinids. Because previous investigation has indicated that Dasyuridae is not currently defined by any dental synapomorphies, caution is demanded regarding allocation of *M. orbus* at the family level. Problems associated with the phylogenetic placement of *M. orbus* portend a story of growing complexity for dasyuromorphian phylogeny — a story progressively being revealed in the Tertiary limestones of Riversleigh.

□ *Mayigriphus*, dasyuromorphian, Miocene, Riversleigh.

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The fossil record for Dasyuromorphia is reviewed by Wroe (1996b, 1997b). Until recently the pre-Pliocene fossil record for Dasyuromorphia was limited to five described taxa, all from deposits in central Australia (*Ankotarinja tirarensis* and *Keeuna woodburnei* (Archer, 1976a), *Wakamatha tasselli* (Archer & Rich, 1979), *Dasyurinja kokuminola* (Archer 1982a) and *Thylacinus potens* (Woodburne, 1967)). With the exception of *Thylacinus potens*, investigation has failed to unequivocally link these fossil taxa with elements of modern dasyuromorphian radiations. More recently, the fossil-rich middle to late Tertiary deposits of Riversleigh have yielded six new thylacinid species: *Nimbacinus dicksoni* (Muirhead & Archer, 1990), *Thylacinus macknessi* (Muirhead, 1992; Muirhead & Gillespie, 1995); *Wabulacinus ridei* (Muirhead, 1997), *Ngamalacinus timmulvaneyi* (Muirhead, 1997), *Badjcinus turnbulli* (Muirhead & Wroe, in press), and *Muribacinus gadiyuli* (Wroe, 1996b). However, only two un-named taxa have been assigned to Dasyuridae: a possible phascogaline taxon known from a single M¹ or M² (Archer, 1982a) and an un-named 'Antechinus-like' species from Riversleigh (Van Dyck, 1989). Wroe (1996b, 1997b) investigates problems with dasyurid phylogeny, concluding that Dasyuridae is currently defined by possibly three basicranial, but no dental synapomorphies. A new dasyuromorphian described here shows an enigmatic combination of features within

Dasyuromorphia and can not be unequivocally assigned at the family level.

Dental nomenclature follows Flower (1867) and Luckett (1993). Taxonomic terminology for Dasyuromorphia follows Wroe (1996b), with three subfamilies recognised within Dasyuridae (Sminthopsinae, Phascogalinae [including *Murexia*], Dasyurinae [including *Neophascogale* and *Phascolosorex*]) and the following taxa considered Dasyuromorphia incertae sedis: *Ankotarinja tirarensis*, *Keeuna woodburnei*, *Wakamathatasselli* and *Dasyurinja kokuminola*. Higher level marsupial systematics follows Marshall et al. (1990). Material is housed in the Queensland Museum (QMF).

SYSTEMATICS

Order DASYUROMORPHIA Gill, 1872
Family INCERTAE SEDIS

Mayigriphus gen. nov.

TYPE AND ONLY SPECIES. *Mayigriphus orbus* gen. et sp. nov.

GENERIC DIAGNOSIS. *Mayigriphus orbus* differs from all dasyurids in the following combination of features: Premolar row compressed longitudinally. P₁ very small; P₃ reduced but with two roots; M₁ compressed on long axis with protoconid central on long and transverse axes with paraconid tiny; M₁₋₄ metaconids and metaconids reduced; M₁ metaconid not differentially reduced relative to M₂₋₄ metaconids;

lingual anterior termination of cristid obliqua on M1-4, with M3 cristid obliqua terminating beneath metaeristid carnassial notch; M1-4 protoconids linguallly shifted and recurved; M1-3 entoconids small to tiny, M4 talonid reduced with entoconid absent. *Mayigriphus orbus* can be distinguished from known thylaciniids by the following combination of features: M1 shows a greatly reduced paraconid but only moderately reduced metaconid; clearly defined hypoconulid notch in anterior cingulid of lower molars; very small size; reduction of P3 relative to P2; lack of diastema between P1 and P2. *Mayigriphus orbus* differs from known bandicoots in possession of the above combination of characters, a well-defined posterior cingulid and more buccally shifted hypoconulid.

ETYMOLOGY. Wanyi *mayi*, tooth; Latin *griphus*, puzzle; refers to the enigmatic combination of dental features. Masculine.

***Mayigriphus orbus* sp. nov.**
(Fig. 1)

ETYMOLOGY. Latin *orbus*, orphan, refers to its uncertain phylogenetic position.

MATERIAL. Holotype, QMF23780, right dentary with partial anterior alveolus of P1, P1 posterior root, P2-3, M1-4; Paratype QMF22791, right dentary fragment containing M3 and alveolus for M4. All from early late Miocene Encore Site, Riversleigh.

DESCRIPTION. Dentary broken away anteriorly from midpoint of P1 anterior root alveolus and posteriorly from about 1 mm along ascending ramus; dentary almost uniform in depth, slight tapering anteriorly from beneath P3 protoconid; mental foramen beneath M1 hypoconid.

P1. P1 crown missing, only posterior half of anterior root alveolus and posterior root remain; based on root and alveolus size P1 small, less than half P2 length; anterior alveolus buccally displaced.

P2. No diastema between P1 and P2; twin rooted; P2 largest premolar in height and length; protoconid moderately worn; buccal cingulid runs posteriorly from midpoint between anterior and posterior roots to small posterior central cuspule on heel; another cingulid circumscribes the lingual crown base from this cuspule to anterior margin of posterior root.

P3. no diastema between P2 and P3; twin rooted; P3 morphology similar to P2 but differs in possession of continuous cingulid circumscribing base

of entire crown and smaller size (P3 around 30 percent smaller in height and length).

M1. no diastema between P3 and M1; M1 unworn; principal cusps in order of decreasing height; protoconid, metaconid, paraconid, hypoconid and entoconid; entoconid tiny, closely abutting posterior face of trigonid adjacent to metaconid; paraconid damaged, but from basal dimensions was clearly small; metaconid small and shifted posteriorly; protoconid dominant cusp, linguallly recurved, occupying almost central position on tooth; M1 reduced on the long axis; talonid small, slightly wider transversely than trigonid but shorter on long axis; paraeristid parallel to, and cristid obliqua shows slight lingual inflection at anterior end; metaeristid and hypocristid parallel and angled at about 20° to transverse axis of dentary; cristid obliqua terminates beneath apex of protoconid; anterior cingulid runs basally from paraconid to beneath protoconid; posterior cingulid weakly developed.

M2. M2 differs from M1 as follows; M2 much larger; paraconid much larger; metaconid relatively and absolutely larger though still small compared to protoconid; talonid shorter on long axis; cristid obliqua terminates against posterior face of trigonid in more lingual position, with angle formed between cristid obliqua and hypocristid more acute; metaeristid and hypocristid run closer to transverse axis of dentary; entoconid relatively larger than in M1 though still small; posterior cingulid more strongly developed; M2 paraeristid runs at about 30° to long axis of dentary, with angle between paraeristid and metaeristid slightly less than 90°.

M3. M3 differs from M2 as follows; protoconid larger; on transverse axis trigonid wider and talonid shorter; entoconid on M3 smaller; cristid obliqua terminates in a more lingual position against posterior face of trigonid beneath carnassial notch of metaeristid.

M4. M4 similar to M3 except: metaconid smaller than paraconid; protoconid less linguallly recurved; talonid greatly reduced, entoconid absent, hypoconid and hypoconulid small; no posterior cingulid.

Meristic gradients from M1-4, orientation of metaeristid and hypocristid to long axis of dentary increasingly transverse from M1-2, departs away from transverse from M2-3, then back to more transverse orientation from M3-4; orientation of paraeristid to long axis of dentary increas-

FIG. 1. *Mayigriphus orbus* sp. nov., QMF23780, holotype. A, buccal view. B and D, stereo-pair, occlusal view of M1-4. C and E, stereo-pair, occlusal view of P1 posterior alveolus, P2-3, M1-4.

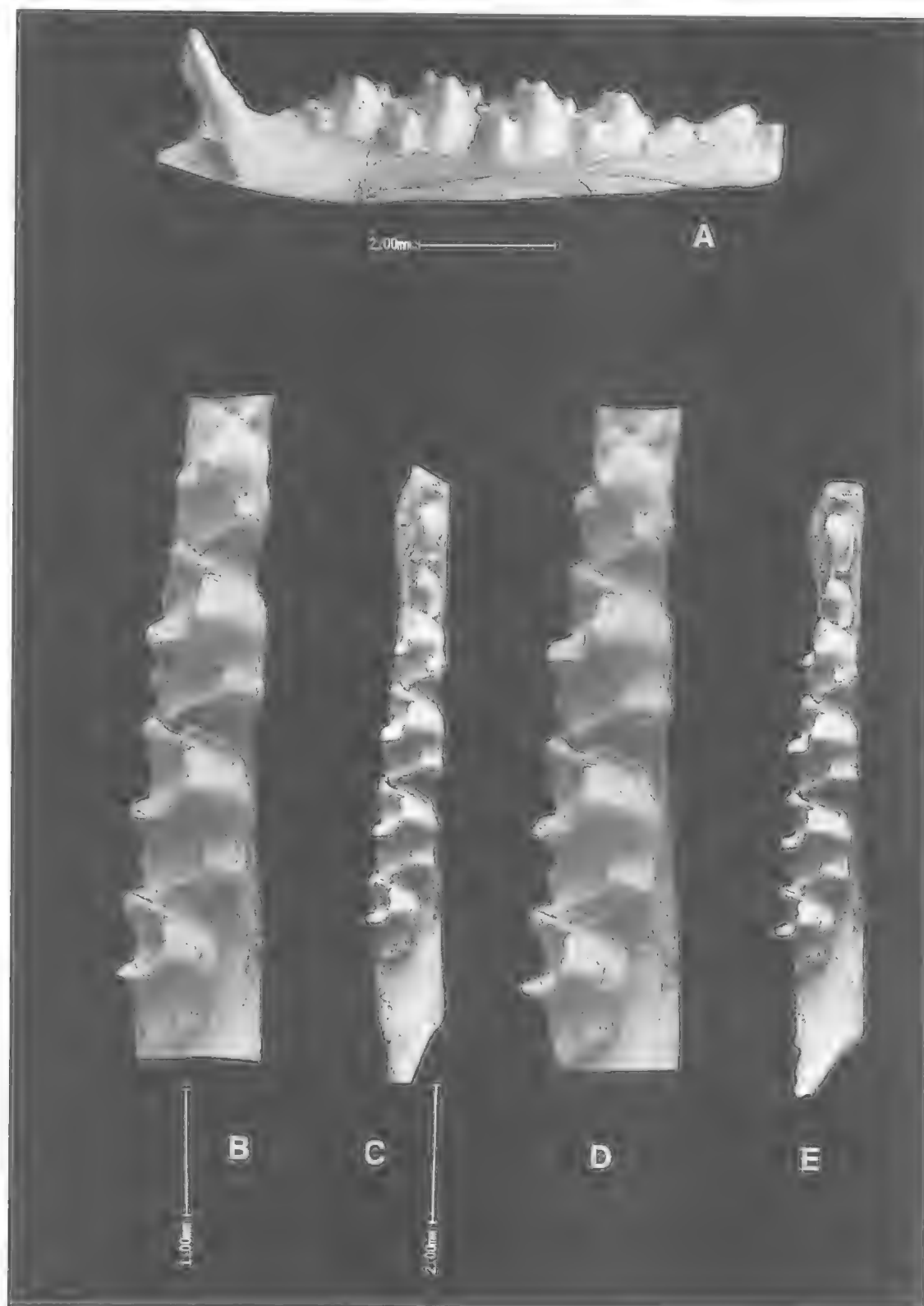


TABLE 1. *Mayigriphus orbus*, dental measurements (mm). l=anteroposterior dimension, w1=maximum transverse dimension of trigonid, w2=maximum transverse dimension of talonid.

Ref no	P ₂		P ₃		M ₁			M ₂			M ₃			M ₄		
	len	wid	len	wid	l	w1	w2	l	w1	w2	l	w1	w2	l	w1	w2
QMF 23780	0.83	0.42	0.67	0.36	1.26	0.64	0.67	1.49	0.84	0.86	1.52	0.84	0.78	1.33	0.74	0.42
QMF 22791											1.45	0.86	0.68			

ingly transverse from M₁₋₃, termination of cristid obliqua against posterior face of trigonid increasingly lingual M₁₋₄; reverses departing from transverse for M₃₋₄; protoconid and metaconid height increases M₁₋₃, decreases M₃₋₄; paraconid height increases M₁₋₄; talonid width increases M₁₋₂, decreases M₃₋₄.

CHARACTER ANALYSIS

Wroe (1996b, 1997b) discusses taxa considered appropriate in the reconstruction of a dasyuromorphian morphotype (i.e., peradeictids, didelphoids, microbintheriids, peramelemorphians). Similar methodology is used for characters treated here to assess character-state polarities (Tables 2, 3). Within Dasyuromorphia *Ankotarinja tirarensis* is the least derived taxon and a possible outgroup to remaining dasyuromorphians. *Muribacinus gadiyuli* and *Badjcinus turnbulli* are the least derived thylacinids. For Dasyuridae the following taxa are considered plesiomorphic for their respective subfamilies: *Murexia longicaudata* (Phascogalinae), *Neophascogale lorentzii* (Dasyurinae) and *Sminthopsis leucopus* (Sminthopsinae).

P₃. A P₃ larger than P₂ is plesiomorphic for outgroups to Dasyuromorphia (Wroe, 1996b, 1997b). For *A. tirarensis* P₃ is slightly smaller than P₂. *Wakamatha tasselli* shows P₃ larger than P₂. The basal thylacinid *Badjcinus turnbulli* has P₃ slightly smaller than P₂. Wroe (1996b) interprets similar P₃ morphology for *Muribacinus gadiyuli* on the basis of alveolar dimensions. For all remaining thylacinid taxa P₃ is larger than P₂, with the largest P₃ in the most derived taxa (*Thylacinus*). Within Dasyuridae wide variation is apparent for this feature. Taxa treated here as basal to their respective subfamilies show a P₃ larger than P₂ (*Murexia*, *Sminthopsis leucopus*), or slightly reduced (*Neophascogale*). However, within each subfamily some taxa show marked reduction or absence of P₃. P₃ reduction in *Mayigriphus orbus* exceeds that shown by all taxa considered Dasyuromorphia incertae sedis, all

Thylacinidae and basal taxa for dasyurid subfamilies.

M₁ paraconid. The M₁ paraconid is not reduced in dasyuromorphian outgroups and *A. tirarensis*. *W. tasselli*, moderate reduction is shown by thylacinids (excepting *B. turnbulli* which shows marked reduction) and plesiomorphic Sminthopsinae (*Sminthopsis leucopus*), Phascogalinae (*Murexia*) and Dasyurinae (*Neophascogale*). M₁ paraconid reduction in *M. orbus* is less marked than in all Dasyurinae excepting *Neophascogale*. For *M. orbus* M₁ shows greater reduction of the paraconid than for all Phascogalinae and Sminthopsinae except *Planigale*.

M₄ talonid. The M₄ talonid is unreduced in basal taxa for Dasyuromorphia except bandicoots (e.g., *Yarala burchfieldi*, Muirhead & Filan, 1995). Within Dasyuromorphia *A. tirarensis*, basal phascogaline (*Murexia*) and dasyurine (*Neophascogale*) taxa show slight reduction for this feature. The M₄ talonid is greatly reduced on the plesiomorphic dasyuromorphian condition for *W. tasselli*, most dasyurines and phascogalines, and all sminthopsines. For thylacinids the M₄ talonid is unreduced for basal taxa (*Muribacinus*, *Badjcinus*), but significantly reduced for derived species (*Thylacinus*, *Wabulacinus*). Even for specialised *Thylacinus* M₄ talonid reduction does not approach that of derived dasyurids which show far greater diminution on the transverse axis. The degree of reduction for this feature in *M. orbus* is closest to that shown in *Phascogale*, but less than for most Dasyurinae, and all Sminthopsinae.

Cristid obliqua orientation. A buccal position for the anterior termination for the cristid obliqua relative to the carnassial notch of the metaacristid is common to most dasyuromorphian outgroup taxa. This feature is associated with cristid obliqua orientation and formation of a right angle between the cristid obliqua and hypocristid. Most outgroup taxa to Dasyuridae and Thylacinidae show a cristid obliqua aligned closely with the long axis of the dentary and a 90° angle is formed between the cristid obliqua and hypocristid. In the

character-analysis (Table 2) only *M*₃ is considered. Buccal termination is shown by *A. tirarensis* and, to a lesser degree, by *K. woodburnei* and *W. tasselli*. Basal thylacinids show relatively lingual anterior termination for the cristid obliqua, but a more buccal position is apparent in *Thylacinus*. Basal dasyurines show lingual termination for the cristid obliqua (*Neophascogale*, *Myoictis*, *Dasyurus hallucatus*), but more specialised taxa show buccal termination (other *Dasyurus*, *Dasyercus*, *Dasyuroides*, *Sarcophilus*). All phascogalines show lingual termination. Sminthopsines show buccal termination. *Mayigriphus orbus* shows lingual termination.

Orientation of the cristid obliqua correlates with other features of both the upper and lower molars. These include the angle between the postparacrista and premetacrista (together termed the centrocrista), the relative size of the protoconid and metaconid and, the occlusal surface area presented by the protocone and talonid basin. Scoring of character states for cristid obliqua without consideration of these associated features may be phylogenetically misleading. For example, derived *Thylacinus* and some dasyurines show longitudinal alignment for the *M*₃ cristid obliqua (unspecialised didelphids, microbiotheriids and *A. tirarensis*), but for these derived dasyuromorphians this feature correlates with protoconid hypertrophy, metaconid reduction or loss, and a linear centrocrista. These character-states are all associated with the dominance of longitudinally oriented vertical shearing crests.

The basal position for Sminthopsinae within Dasyuridae indicated by molecular analyses (Kirsch et al, 1990; Krajewski et al., 1993; 1994) supports the contention that a buccal point of termination for the cristid obliqua is a plesiomorphy for the clade. However, dental features of Sminthopsinae are products of a different selective regime and transverse rather than longitudinal vertical shearing crests dominate. Archer (1976) noted that a buccal position for the cristid obliqua may be associated with reduction of the paracone or a lingual shift in the carnassial notch (of the metacristid). Both derived features are shown by sminthopsines and it is probable that cristid obliqua position represents a correlated apomorphic feature. A further derived feature shown by sminthopsines is gross reduction of the talonid on the anteroposterior axis which may also impact on cristid obliqua orientation. For sminthopsines and derived dasyurines and thylacinids, a buccal position for the cristid obliqua is treated as derived relative to that of microbio-

theriids, unspecialised didelphids, bandicoots and *A. tirarensis* (Tables 2, 3). A relatively more lingual termination for the cristid obliqua, as shown by most dasyurids and basal thylacinids, is also considered derived. The character complex associated with most dasyurids (a relatively lingual anterior termination point and acute angle formed between the cristid obliqua and hypocristid) is scored as 'a'. Buccal termination and formation of 90° between the cristid obliqua and hypocristid may be associated with increased transverse vertical shear (b) or increased longitudinal vertical shear (c).

Angle between paracristid and metacristid. For dasyuromorphian outgroups an acute angle is formed between the paracristids and metacristids (mirrored by an equivalent angle formed between the postmetacristae and preprotocristae with which they occlude in the upper dentition). Similar morphology is shown by *A. tirarensis*, *W. tasselli* and sminthopsine dasyurids. All dasyurines, phascogalines, basal thylacinids for which a metacristid is retained, and *M. orbus* show a relatively obtuse angle between paracristids and metacristids. Widest paracristid-metacristid angles are in *Sarcophilus*, *Glaucodon* and *D. maculatus* among dasyurids and *Ngamalacinus* among thylacinids. This phenomenon is correlated with carnivory and the development of longitudinally aligned vertical shearing crests.

Hypoconulid notch. Many marsupials have a distinct notch in the anterior cingulae of their lower molars to receive the hypoconulid of the preceding tooth. Outgroup data for Dasyuromorphia regarding this feature is equivocal. Some outgroup taxa (e.g., some peradectids) show a well-developed hypoconulid notch, but among other possible outgroups this feature is absent (e.g., peramelemorphs). Within Dasyuromorphia this feature is well-developed for *Ankotarinja tirarensis* and *Keeuna woodburnei*, but poorly defined for *Wakamatha tasselli* (see Wroe (1996b) re arguments for possible bandicoot affinities of this taxon). Among thylacinids, a well-developed hypoconulid notch is present for *Muribacinus* and *Badjcinus*, weakly-defined in *Ngamalacinus*, and absent in all other taxa. A well-developed hypoconulid notch occurs in all dasyurids excepting *Dasyurus maculatus* (reduced), and *Glaucodon* and *Sarcophilus* (absent). *Mayigriphus orbus* has a well-defined hypoconulid notch. Wroe (in press b) infers that loss of the hypoconulid notch is a function of ad-

TABLE 2. Characters and character-states used in phylogenetic analysis.

C1. P ₃ size relative to P ₂ . 0. larger. 1. reduced. 2. intermediate. 3. tiny. 4. absent.
C2. M ₁ paraconid size. 0. large. 1. reduced. 2. tiny. 3. absent.
C3. M ₄ talonid size. 0. large. 1. moderately reduced. 2. markedly reduced. 3. tiny.
C4. M ₁ cristid obliqua morphology. [†] P. plesiomorphic. a. lingual. b. trans. shear. c. long. shear.
C5. Angle between paracristid-metacristid. 0. acute. 1. intermediate. 2. obtuse.
C6. Hypoconulid notch. 0. well developed. 1. intermediate. 2. absent.
C7. Metaconid morphology. 0. no clear differential between M ₁ and M ₂₋₄ . 1. clear differential.
C8. M ₂₋₄ metaconid size. 0. large. 1. reduced. 2. greatly reduced. 3. absent.
C9. M ₃ entoconid size. 0. large. 1. reduced. 2. absent.

[†] Three derived states recorded for this character (see text).

vanced carnassialisation for derived dasyurids and thylacinids, noting that the shift to a predominance of longitudinal vertical shear in marsupial carnivores diminishes the requirement for a brace against transverse forces (i.e., the likely role for the hypoconulid notch).

Archer (1982b) regarded a hypoconulid notch in the anterior cingulum as a possible dasyurid synapomorphy. But Wroe (1997) concludes that it may have been in the common ancestor of Dasyuromorphia and was almost certainly in the common ancestor of Dasyuridae-Thylacinidae. For specialised dasyurids (*Sarcophilus* and *Glaucodon*) and thylacinids (*Thylacinus*, *Wubulacinus*) loss of the hypoconulid notch correlates with advanced carnassialisation.

Metaconid. A well-developed metaconid on all lower molars occurs in all putative Dasyuromorphian outgroups. The same is so for *A. tirarensis*, *K. woodburnei* and *W. tasselli*. All thylacinids show marked reduction or loss of the metaconid on all lower molars. Among Dasyuridae this feature is variable. Plesiomorphic taxa for each subfamily show no reduction of the metaconids. However, specialised Dasyurinae and Sminthopsinae show derived character-states. Derived dasyurines show a reduced M₁ metaconid, but less reduction for M₂₋₄ metaconids (*Dasyercus*, *Dasyuroides*, *Dasyurus*, *Sarcophilus*). In *Planigale* metaconid diminution is less advanced on M₁ and more uniform through M₂₋₄. This phenomenon shown for *Planigale* is also common to thylacinids which retain metaconids (except *Badjcinus turnbulli* which shows the typical dasyurine condition). *Mayigriphus orbus* shows uniform reduction of M₁₋₄ metaconids, the character-state common to *Planigale* among dasyurids and *Muribacinus*, *Nimbacinus* and *Ngamalacinus* among thylacinids.

Localised metaconid reduction (i.e., a clear differential shown between M₁ and M₂₋₄ metaconid reduction) as shown by some dasyurines, sminthopsines and *Badjcinus*, is probably related to brachycephalisation, shortening of the tooth row on the anteroposterior axis and concomitant premolarisation of M₁ (Archer, 1976). Generalised metaconid reduction (M₁₋₄) correlates with increased size of the protoconid and primacy of the paracristid and postmetacristae in vertical shear. For carnivorous dasyurids and thylacinids these derived features are associated with alignment of the vertical shearing crests with the long axis of the tooth row.

Entoconid. Large entoconids are plesiomorphic for dasyuromorphian outgroups, *A. tirarensis*, *K. woodburnei*, basal dasyurines and sminthopsines, and phascogalines. Entoconids are reduced or absent in some *Sminthopsis* and *Antechinomys* among sminthopsines and *Parantechinus*, *Pseudantechinus*, *Dasyuroides*, *Dasyercus*, *Dasykaluta*, most *Dasyurus* (excepting *D. hallucatus*), *Sarcophilus* and *Glaucodon*. All thylacinids show some entoconid reduction, with the least reduction in *Muribacinus* and the greatest by *Thylacinus*. *Mayigriphus orbus* shows moderate reduction for this feature. Archer (1981) and Sanson (1985) note that no clear form-function relationship explains the distribution of entoconid reduction and loss among dasyurids, but note that this reduction is greatest for arid-adapted species (some *Sminthopsis*, *Antechinomys*, *Dasyuroides*, *Dasyercus*). However, considerable reduction or loss is shown for some species found in less extreme environments and for large dasyurid and thylacinid carnivores this phenomenon is likely associated with carnivory. More form-function data is required here.

TABLE 3. Character/taxon matrix.

<i>Mayigriphus orbus</i>	211a2	0011
<i>Alphadon marshi</i>	00000	0000
<i>Marmosa</i> sp.	00000	0000
<i>Didelphis marsupialis</i>	10000	0000
<i>Dremiclops australis</i>	00100	1000
<i>Yarala burchfieldi</i>	00200	2000
<i>Ankotarinja tirarensis</i>	10000	0000
<i>Keeuna woodburnei</i>	???a1	0?00
<i>Wakamatha tasselli</i>	0?200	1?00
<i>Muribacinus gadiyuli</i>	110a2	0010
<i>Badjcinus tarnbuli</i>	110a2	0110
<i>Nimbacinus dicksoni</i>	701?2	?01?
<i>Ngamalacinus timmulvaneyi</i>	701c1	1020
<i>Wabulacinus ridei</i>	077c2	1?22
<i>Thylacinus macknessi</i>	001c?	1?31
<i>Thylacinus cynocephalus</i>	002c2	1032
<i>Sminthopsis leucopus</i>	102b0	0002
<i>Planigale maculata</i>	213b0	0012
<i>Planigale gilesi</i>	313b0	0012
<i>Planigale teniostris</i>	213b0	0012
<i>Murexia longicaudata</i>	011a1	0000
<i>Phascogale tapoastfa</i>	101a1	0000
<i>Neophascogale lorentzii</i>	101a1	0000
<i>Myoictis melas</i>	121a1	0000
<i>Purantechnus apicalis</i>	223c1	0102
<i>Dasyurus hallucatus</i>	322a1	1110
<i>Dasyurus maculatus</i>	322c2	2121
<i>Sarcophilus harrisii</i>	323c2	2121

DISCUSSION

BIOSTRATIGRAPHY AND ECOLOGY. To date *M. orbus* is restricted to early late Miocene Archer et al. (1995) Encore Site at Riversleigh. Encore has produced a fauna that includes several unique taxa, including a large dasyuromorphian of uncertain affinity (unpubl. data), a giant *Ekaltadeta* (Wroe, 1996a), a derived koala (Black, pers. comm.), a palorchestid structurally intermediate between species from Riversleigh System C and the late Miocene *Palorchestes painei* of Alcoota (Black, 1997) and a *Warenja*-like wombat (Archer et al., 1995). The rootless teeth of this wombat (unknown for other species at Riversleigh) and the relatively low abundance of the frog *Lechriodus intergervis*, common in other Miocene Riversleigh deposits (Godthelp, pers. comm.) indicate that climatic conditions may have been drier for the depositional episode

during which Encore was produced. Tentative support for a relatively late age for Encore site, is also forwarded by Wroe (1997a). If *M. orbus* is a dasyurid then the derived dentition (relative to other Miocene dasyurids) might also suggest a late age for Encore site. As noted above for small dasyurids, circumstantial evidence correlates entoconid reduction with adaptation to relatively dry environments.

Mayigriphus orbus is the smallest dasyuromorphian from the Oligocene and Miocene of Riversleigh and is comparable to *Planigale maculatus* in size. Only one other marsupial insectivore has been identified that might have competed closely with *M. orbus*, the diminutive bandicoot *Yarala burchfieldi* (Muirhead, 1995). As with modern *Planigale* (Denny, 1982) the diet of *M. orbus* probably included invertebrates, frogs, small lizards and/or small mammals.

PHYLOGENY. *Mayigriphus orbus* shows a unique mosaic of features among dasyuromorphians. Two features of *M. orbus* may indicate a relationship with *Planigale* (the greatly reduced M1 paraconid concurrent with a moderately reduced M1 metaconid, and relatively uniform diminution of the M1-4 metaconids). Although a comparable degree of M1 paraconid reduction is also common to many derived dasyurines (e.g., *Pseudantechnus*), in these taxa diminution of the M1 metaconid is far more advanced and a clear differential is produced between that shown by M1 and M2-4. Additional apomorphies shared by *M. orbus* and *Planigale* (e.g., reduction of M4 talonid, entoconid and P3), are also found in other specialised dasyurid taxa. On the basis of cytochrome-b data, Painter et al. (1995) estimate the oldest branchings within *Planigale* at 11-15 mya, thus the possibility that *M. orbus* represents an early branch of this radiation can not be discounted. However, *M. orbus* shows at least 2 derived features not in *Planigale* (wide angle formed between the paracristid, metacristid, a buccal shift in the point of termination of the cristid obliqua). The oldest material clearly attributable to *Planigale* is Pliocene (Archer, 1982a). Based on available data, a sister taxa association for *M. orbus* with *Planigale* is considered equivocal.

Even at the family level, the phylogenetic position of *M. orbus* is considered uncertain, because it has a number of features that might be interpreted as synapomorphies for either derived dasyurid or thylacinid clades, but no unequivocal synapomorphies (within Dasyurn

morphia) for either family. Two synapomorphies for the Dasyuridae are in the lower dentition of *M. orbus*: reduction of P_3 (Tate, 1947; Archer, 1982b; Marshall, 1990) and the hypoconulid notch in the lower molars (Archer, 1982b). Status of both as shared-derived features for Dasyuridae is questioned by Wroe (1996b, 1997b). Reduction of P_3 is certainly common within Dasyuridae which culminates in the loss of this tooth among specialised taxa. However, reduction or loss of P_3 may have occurred independently at least 3 times in the Dasyuridae (Archer, 1981). A further argument against the phylogenetic value of this character at the family level is the P_3 smaller than P_2 in 2 thylacinids from Riversleigh (Muirhead & Wroe, in press; Wroe, 1996b, 1997b). The status of the hypoconulid notch as a shared derived feature for dasyurids has been undermined by the discovery of plesiomorphic thylacinids with a well-defined hypoconulid notch in the lower molars (Wroe, 1997b; Muirhead & Wroe, in press). Marked reduction of the M_1 paraconid in *M. orbus* is common to specialised dasyurids but not thylacinids, excepting *Badjcinus turnbulli* (Muirhead & Wroe, in press). None of these features represent unequivocal synapomorphies for Dasyuridae and each have been independently derived within specialised dasyurid lineages. At least 3 features in *M. orbus* suggest a possible alliance with thylacinids. Firstly, the lack of a clear differential between metaconid reduction on M_1 and M_{2-4} in *M. orbus* is known only for *Planigale* among dasyurids but common to plesiomorphic thylacinids. In all dasyurids except *Planigale*, M_1 metaconid reduction clearly exceeds that of M_{2-4} . Although reduction of the M_{2-4} metaconids is less pronounced in *M. orbus* than in known thylacinids, excepting *Muribacinus*, it is greater than for most dasyurids except *D. maculatus*, *Sarcophilus* and *Planigale*. Secondly, the wide angle formed between the paracristid and metacristid in *M. orbus* is found in basal thylacinids, but only *D. maculatus*, *Sarcophilus* and *Glaucodon* among dasyurids. Thirdly, among specialised dasyurids, reduction of the M_{1-4} talonids and metaconids is commonly associated with a buccal shift in the point of termination of the cristid obliqua. In both *M. orbus* and plesiomorphic thylacinids this is not the case, with the cristid obliqua terminating in a relatively lingual position. Ultimately, this may be related to Ride's (1964) observation of a difference between *Thylacinus* and specialised dasyurids in the composition of the principal posterior shearing crest. Ride pointed out that, in

Thylacinus, the posterior shearing crest runs from the protoconid directly to the hypoconid, while in derived dasyurids (especially *Sarcophilus*) the posterior shearing crest connects the protoconid and metaconid.

CONCLUSIONS

If *M. orbus* is a dasyurid it represents the most derived member of the family known from pre-Pliocene times, with the possible exception of the Miocene *Dasyurinja kokuminola* (Archer, 1982a) from Lake Yanda in central Australia. A special relationship between these two taxa can not be discounted, with both showing specialisations associated with carnassialisation (the much larger size of *D. kokuminola* precludes the possibility that the 2 taxa are conspecific). *D. kokuminola* is known only from a single upper molar and direct comparisons with *M. orbus* cannot be made. Among known dasyurids *M. orbus* shares the greatest number of derived features with *Planigale*: two character-states (disparate reduction of the M_1 paraconid and metaconid and uniform reduction of the M_{1-4} metaconids) suggest the possibility of a special relationship for the 2 taxa. However, uniform diminution of the M_{1-4} metaconids is also shown by some basal thylacinids.

Mayigriphus orbus shows no unequivocal synapomorphies for either dasyurid or thylacinid clades. For Dasyuridae, unique derived-features (within Dasyuromorphia) are only found in the basicranium (Wroe, 1996b, 1997b). Unique derived features (within Dasyuromorphia) uniting Thylacinidae have been identified only in the upper dentition (Wroe, 1996b). Neither region is known for *M. orbus*. Confident phylogenetic assignment for *M. orbus* has been further tempered by the identification of possible thylacinid apomorphies in this taxon, which must be considered in the following context: investigation of Oligocene and Miocene material from Riversleigh is revealing a complex dasyuromorphian phylogeny dominated by a diverse thylacinid clade, showing greatly expanded intrafamilial variation (Muirhead, 1992, 1997; Muirhead & Archer, 1990; Muirhead & Wroe, in press; Wroe, 1996b, 1997b) a close relationship between Dasyuridae and Thylacinidae has been established by molecular studies (Lowenstein et al., 1981; Sarich et al., 1982; Thomas, 1989; Krajewski et al., 1992), and a relatively recent genesis for Dasyuridae has been suggested (Archer, 1982a; Krajewski, 1992; Wroe, 1996b,

1997b). Given this emerging climate of complexity for dasyuromorphian phylogeny, the curious mix of derived features in *M. orbus* (otherwise considered diagnostic of either specialised dasyurid or thylacinid clades) makes reliable placement within either family impossible, particularly as this decision must currently be based solely on elements of the lower dentition. Problems associated with determining the phylogenetic position of *M. orbus* highlight an unexpected phylogenetic scenario. Despite an abundance of dasyuromorphian material from Oligocene-Miocene deposits of Riversleigh no taxon has yet been described which can be unequivocally associated with elements of the now ubiquitous dasyurid radiation.

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STRATIGRAPHY AND PHYLOGENY OF THE GIANT EXTINCT RAT-KANGAROOS (PROPLEOPINAE, HYPSPRYMNODONTIDAE, MARSUPIALIA)

S. WROE

Wroe, S. 1997 06 30: Stratigraphy and phylogeny of the giant extinct Rat-kangaroos (Propleopinae, Hypsiprymnodontidae, Marsupialia). *Memols of the Queensland Museum* 41(2): 449-456. Brisbane. ISSN 0079-8835.

The Giant Rat-kangaroos were placed in the Propleopinae by Archer & Flannery (1985) and in the Hypsiprymnodontidae by Ride (1993). Cladistic analysis of *Ekaltadeta* material from Riversleigh, northwestern Queensland (Wroe, 1996) suggested that a middle to late Miocene dichotomy in *Ekaltadeta* may have produced two lineages of Plio-Pleistocene *Propleopus*, indicating polyphyly for *Propleopus* and paraphyly for *Ekaltadeta*. Metrical data for propleopines and stratigraphic information support Wroe's (1996) cladistic analysis of propleopines. □ *Propleopinae, Hypsiprymnodontidae, Riversleigh, Ekaltadeta, cladistics.*

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Giant Rat-kangaroos (Hypsiprymnodontidae: Propleopinae) may be the plesiomorphic sister group of potoroids (Flannery, 1987). Archer & Flannery (1985) considered *Ekaltadeta ima*, (Fig. 1) the sister group to *Propleopus* De Vis, 1888 with *P. oscillans* De Vis, 1888 (Fig. 2) the more plesiomorphic and *P. chillagoensis* Archer et al. (1978) (Fig. 2) the more apomorphic within *Propleopus* (Fig. 3). Propleopine species described since 1985 are *Ekaltadeta jamiemulvaneyi* Wroe, 1996, (Fig. 4) and *Jackmahoneya toxoniensis* Ride, 1993. Wroe (1996) suggested another possible phylogeny for the Propleopinae with *E. ima* and *P. chillagoensis* forming the sister group to another clade containing a new species, *E. jamiemulvaneyi*, as the sister taxon to *P. wellingtonensis* and *P. oscillans*. (Fig. 5). As an adjunct to the cladistic analysis (Wroe, 1996), metric and stratigraphic data for propleopines are used to clarify intrasubfamilial relationships.

Dental homology for premolars follows Flower (1867) and Luckett (1993) for molars. Higher level systematics of kangaroos follows Flannery (1987) and Ride (1993). Specimens are housed in the Queensland Museum (QMF). Other prefixes include; UCM (University of California Museum), NMV (Museum of Victoria).

METHODS

Specimens of *Ekaltadeta* from Riversleigh represent 30 individuals from several stratigraphic levels. The relative paucity of specimens and chronological data precludes a strictly stratophenetic approach (*sensu* Gingerich, 1976, 1979; Bown & Rose, 1987) to propleopine phylogeny.

However, a more general consideration of stratigraphy in phylogenetic analysis may be appropriate in association with cladistic treatment where specimens are stratigraphically disjunct or sparsely distributed (Gingerich, 1990).

Sites with *Ekaltadeta* are late Oligocene to early late Miocene (Archer et al., 1989, 1994, 1995). A number of characters were analysed to assess the development of time-dependent changes. Specimens were ranked to indicate relative age (Appendix 1). Stratigraphic levels are from Archer et al. (1989, 1995): level 1=late Oligocene early Miocene; level 2=early Miocene; level 3=late early Miocene; level 4=mid Miocene; level 5=late mid Miocene; level 6=early late Miocene; level 7=Pliocene; level 8=Pleistocene.

I included all propleopines possible, although Pliocene and Pleistocene *Jackmahoneya* and *Propleopus* are known from material often limited to portions of upper and/or lower dentitions. Most *Propleopus* are from the Pleistocene, although material has been recorded from early Pliocene local faunas (Archer & Flannery, 1985). *Propleopus chillagoensis* was described as Pleistocene (Archer et al., 1985), but could be older, possibly late Miocene or early Pliocene (Archer pers. comm.). *Jackmahoneya toxoniensis* is Pliocene (Ride, 1993).

Differences in molar gradient were used by Archer & Flannery (1985) and Wroe (1996) to distinguish propleopine species. Molar gradient reflects both the surface area and length of the molar tooth row. In propleopines a high molar gradient correlates with a reduction in both molar surface area and the length of the tooth row.

Reducing the distance between condyle and sectorial tooth maximizes leverage applicable to the tooth (Young et al., 1989). Through shortening the molar row, leverage on the large shearing $P^3/3$ of propleopines is increased. This effect is achieved at the cost of molar length.

Relative P_3 size and molar gradient for upper and lower dentitions has been quantified. Distinct reduction in tooth size posteriorly occurs in upper and lower dentitions of *E. ima*. In the upper dentition this steep gradient begins with a reduced posterior width (pw) relative to the anterior width (aw) of M^2 which then ramifies through M^{3-4} . In *E. ima* M^4 pw is $<1/2$ M^2 aw. The upper dentition of *P. chillagoensis* is similar to that of *E. ima*. Lower dentition is not known for *P. chillagoensis*. For *P. oscillans* M^{3-4} are missing but M^2 pw is only slightly less than M^2 aw suggesting a less extreme gradient. This supposition is strongly supported by the lower dentition in which molar gradient contrasts strongly with *E. ima*. M_{1-4} tooth widths decrease steadily anteroposteriorly in *E. ima* but are reversed in *P. oscillans* where tooth width increases posteriorly for M_{1-3} , with only a slight decrease in M_4 .

Several methods to quantify molar gradient have been considered. Accurate determination of individual molar surface areas and comparisons between teeth would be useful but would require 2 or more teeth/ specimen, greatly limiting data sets, particularly for upper dentitions. Molar gradient might also be estimated geometrically by determining the angle at which a line drawn buccally or lingually through the faces of the crown intersects the mid-line of the dentary or skull.

In this study the clear initiation of a marked molar gradient at M^2 in the upper dentitions of *E. ima* and *P. chillagoensis* permitted estimation of the gradient from a single molar by comparing aw to pw. In lower dentitions the gradient is less



FIG. 1. *Ekaltadeta ima*, x 2. A, oclusal view of QMF12436 (uppers). B, buccal view of QMF12435, left dentary containing I_1 , alveolus for I_2 , P_{2-3} , M_{1-4} . C, oclusal view of QMF12435.

distinct and 2 molars were required to demonstrate a gradient. Measurements were made using a Wild MMS 235 Digital Length-Measuring Set attached to a Wild M5A Stereomicroscope. Abbreviations are: l=length, w=width, aw=anterior width, pw=posterior width, dd=depth of dentary, G-value=ratio of anterior to posterior tooth width.

RESULTS

M^2 aw / M^2 pw VS STRATIGRAPHIC LEVEL. (Fig. 6). For upper dentitions the ratio M^2 aw: M^2 pw (G-value) was used as an arbitrary measure of molar gradient, with M^2 being common to the largest number of specimens.

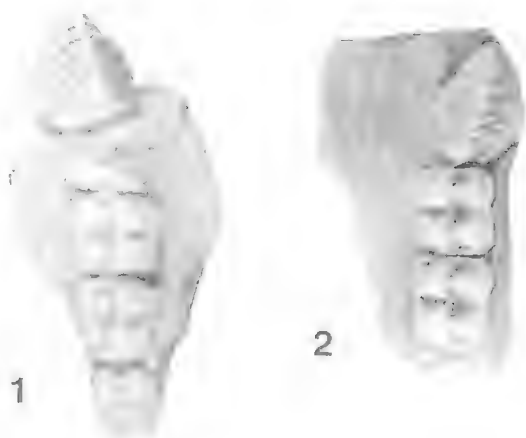


FIG. 2. *Propleopus chillagoensis*, x 2. A, occlusal view of NMV P15917, right maxillary fragment (juvenile), containing unerupted P³, partial M¹, M²⁻³, partial M⁴ (cast of holotype). B, *Propleopus oscillans*, x 2, occlusal view of QMF6675, left maxillary fragment, containing P³, M¹⁻².

A trend is apparent in this scatter graph of G-value against stratigraphic level. *P. chillagoensis* and *P. oscillans* represent 2 extremes with G-values of 1.23 and 1.06 respectively, with the lower number indicating a lesser molar gradient. *Ekaltadeta ima* from levels 3 and 4 has a limited range of G-values (1.09-1.15).

The 2 *Ekaltadeta* from level 6 both fell outside the range of *E. ima* from older strata. *E. jamiemulvaneyi* (QMF24212; Cleft of Ages 4 Site) had a low G-value of 1.05, slightly less than that of *P. oscillans*. *E. ima* (QMF24211; Henk's Hollow Site) had a relatively high G-value of 1.19 approaching that of *P. chillagoensis*. These results indicate a divergence in the *Ekaltadeta* lineage with one population leading to *P. oscillans* and another leading to *P. chillagoensis*.

M₁ pw / M₂ pw VS STRATIGRAPHIC LEVEL. (Fig. 7). The molar gradient of the dentary was estimated by dividing M₁ pw by M₂ pw (G-value). *P. oscillans* had the lowest G-value at 0.93. The G-values for *P. wellingtonensis* and *J. toxoniensis* were slightly higher at 0.96. At levels 3 and 4 the G-values for *Ekaltadeta* were 1.01-1.08. The G-value for *E. jamiemulvaneyi*, from level 6 (QMF24200, Encore Site) was 0.97. This placed *E. jamiemulvaneyi* about halfway between the lowest G-value from levels 3 and 4 and *P. oscillans*. Again the highest degree of divergence among *Ekaltadeta* was for the *E. jamiemulvaneyi* from level 6, possibly indicating a trend toward

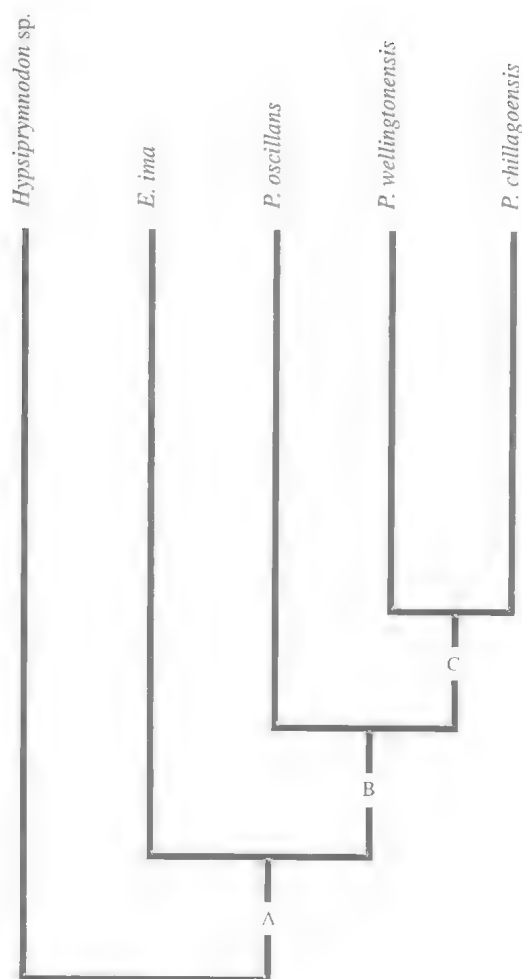


FIG. 3. Cladogram for the propleopines from Archer & Flannery (1985). Character states at nodes: A=gain of an anterior cristid emanating from the metaconid of M₁, gain of derived I₁ morphology; B=incorporation of the protolophid into the anterior lophid of M₁ loss of P₂ with eruption of P₃, dentary deeper anteriorly than posteriorly; C=reduction of metacone/entoconid, P₃ hypertrophy.

the species with low molar gradients (*J. toxoniensis*, *P. oscillans* and *P. wellingtonensis*).

P₃ w/M₁pw VS STRATIGRAPHIC LEVEL. (Fig. 8). In *P. oscillans* P₃ width was small compared to M₁ posterior width (1.09). For *J. toxoniensis* relative P₃ width was greater (1.27). *E. ima* from levels 3 and 4 had ratios of P₃ w / M₁ pw of 1.35-1.52. *E. jamiemulvaneyi* from Encore

site (QMF24200) again positioned between *E. ima* from lower strata and *J. toxoniensis* / *P. oscillans*, with a ratio of 1.28

DEPTH OF DENTARY AGAINST STRATIGRAPHIC LEVEL.

Depth of dentary against stratigraphic level (Fig. 9). Dentary depth was measured from the alveolar margin of M_1 to the ventral margin of the dentary perpendicular to the molar row. Variation in the depth of dentaries was small for *E. ima* from levels 3 and 4 (19.3–21.1mm). *E. jamiemulvaneyi* (QMF24200) was much larger with a dentary depth of 28.8mm approaching *P. oscillans* (32.6mm). *J. toxoniensis* between *E. ima* and *E. jamiemulvaneyi*/*P. oscillans* with a dentary depth of 23.3mm.

STATISTICAL ANALYSIS.

(Table 1). Because all *Ekaltadeta* material has come from a relatively small area (Riversleigh), a regional population of potoroids was considered an appropriate control. Sixteen specimens from the Australian museum of *Potorous tridactylus* collected around Hobart were used, this being the largest potoroid specimen sample available. Variation in the G-values of *Ekaltadeta* from levels 3 and 4 approached that of *P. tridactylus*. When G-values from the 2 *Ekaltadeta* from level 6 were included the variation fell well outside that of the local *P. tridactylus* population.

DISCUSSION

Increases in premolar and molar shear within the Proploepinae appear to be mutually exclusive and their relative importance probably reflects dietary preference. A requirement for high premolar shear might be associated with carnivory

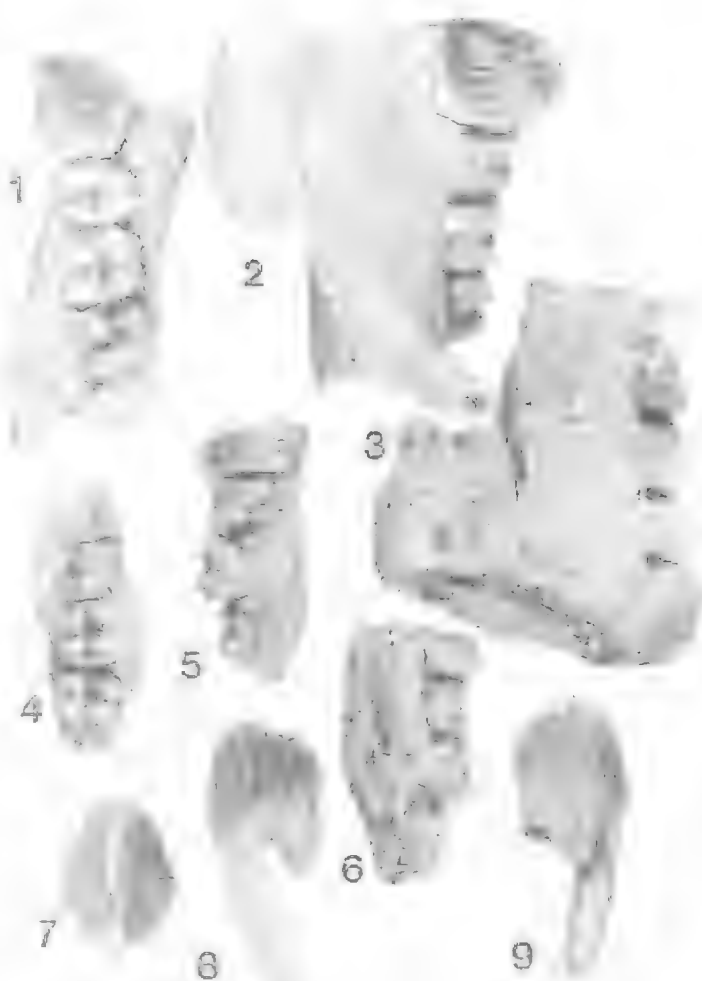


FIG. 4. *Ekaltadeta jamiemulvaneyi* x 2. A, occlusal view of QMF24200, left dentary containing P_3 , M_{1-3} , holotype. B, buccal view of QMF24200. C, lingual view of QMF24200. D, occlusal view of QMF24212, left maxillary fragment, containing P_2 , dP_3 , M_{1-2} , referred specimen. E, buccal view of QMF24212. F, lingual view of QMF24212. G, occlusal view of QMF20842, left P_3 , referred specimen. H, buccal view of QMF20842. I, lingual view of QMF20849.

(Abbie, 1939), while a more extensive molar array may indicate a more herbivorous diet (Wells et al., 1982).

Species with a large molar surface area and low molar gradient (*P. oscillans*, *P. wellingtonensis*, *J. toxoniensis*) have relatively small premolars. Species with high molar gradients and reduced molar shear (*E. ima*, *P. chillagoensis*) are characterised by P_3 hypertrophy. The extraordinary change in function for P_2 shown by individ-

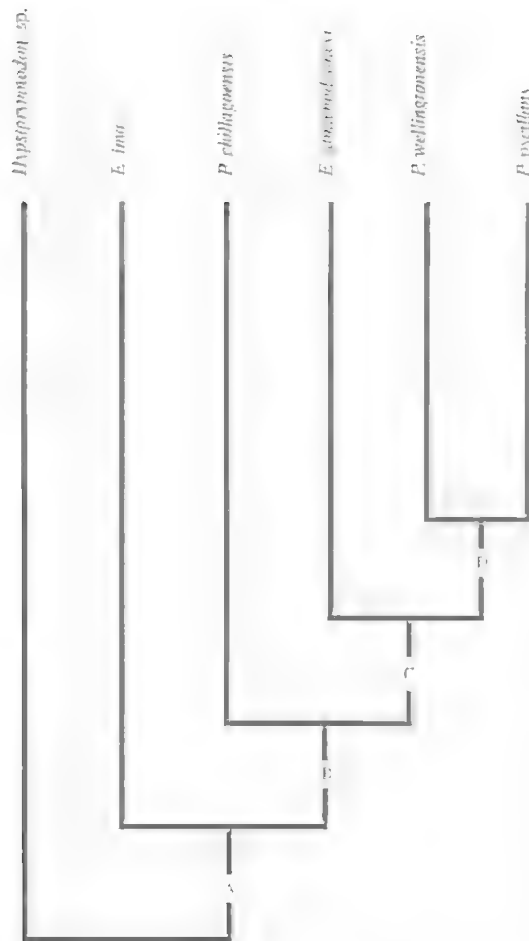


FIG. 5. Minimal tree produced by Wagner analysis for the Propleopinae (from Wroe, 1996). Character states at nodes: A = gain of an anterior cristid emanating from the metaconid of M_1 ; basally broad conical upper molars; B = presence of lingual cingula on the upper molars; C = reduced molar gradient, reduced P_3 ; D = incorporation of the protolophid into the anterior lophid of M_1 , a dentary deeper posteriorly than anteriorly.

ual *E. ima* (Wroe & Archer, 1995) probably constitutes a response to the increased loading placed on P_3 . Regarding molar gradient and relative size of the P_3 , *E. jamiemulvaneyi* is intermediate, falling between *E. ima* specimens from lower levels and *P. oscillans*/*P. wellingtonensis*/*J. taxoniensis*. Using the same criteria *J. taxoniensis* lies between *E. jamiemulvaneyi* and *P. oscillans*/*P. wellingtonensis*. In terms of variation in P_3 size and molar gradient *P. chillagoensis* and *P. oscillans* represent opposite extremes in propleopine evolution and it is suggested that *P. oscillans*

TABLE 1. Statistical summaries for M^2_{aw} / M^2_{pw} (G-value) for propleopines and a local *P. tridactylus* population.

	N	SD	CV	SE
Propleopines to level 8	13	0.05	4.53	0.01
<i>Ekaltadeta</i> to level 6	11	0.38	3.35	0.01
<i>Ekaltadeta</i> to level 4	9	0.02	2.07	7.71 E-3
<i>P. tridactylus</i>	16	0.02	1.70	4.61 E-3

was largely if not wholly herbivorous. Other derived features interpreted as adaptations to herbivory for *P. oscillans* include a large diastema between P_3 and I_1 , and large spatulate lower incisors (Wroe, 1996). Regarding dentary depth *E. ima* is the smallest propleopine with a general increase in depth for taxa at higher stratigraphic levels probably reflecting a general increase in body size.

Stratigraphic and metric analysis support the proposal of a late Miocene dichotomy in *Ekaltadeta* producing 2 lineages of *Propleopus*, and a reversal of previous assumptions on relative apomorphy within *Propleopus*, with *P. oscillans* considered the most derived and *P. chillagoensis* the most plesiomorphic (Wroe, 1996). However, broad trends suggested in this study are not interpreted here chronoclines in the stratophenetic sense (*sensu* Bown & Rose, 1987). The scarcity of material and uncertain chronology of both the Oligo-Miocene Riversleigh deposits and the Plio-Pleistocene local faunas from which most propleopine specimens are known necessitates caution in the interpretation of results. A considerable temporal gap exists between estimated ages of the most recent *Ekaltadeta* specimens and all other propleopines. As noted by Ride (1993), the period separating the latest known incidence of *Ekaltadeta* from Plio-Pleistocene *Propleopus* and *Jackmahoneya* may be sufficient to have permitted a secondary reversal of character states within *Propleopus* to produce *P. chillagoensis*.

Many questions remain concerning the age, stratigraphy and method of deposition of Riversleigh's Oligocene-Miocene limestone deposits (Archer, 1994, 1995; Megirian, 1992, 1994). If the phylogeny for propleopines suggested by Wroe (1996) reflects evolutionary events, then it provides tacit support for Archer et al.'s (1989) proposed stratigraphy, with an agreement of hypothesised superpositional and phylogenetic patterns.

The capacity of stratigraphic occurrence to explicitly mirror phylogenies is questionable (Engelmann & Wiley, 1977). Although strong

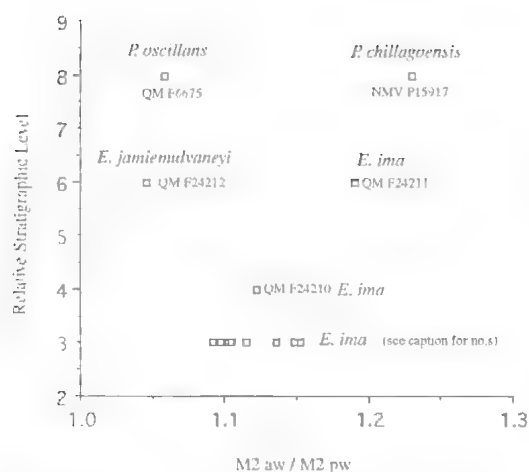


FIG. 6. M^2 aw / M^2 pw vs relative stratigraphic level for propleopines. *Ekaltadeta ima* from level 3, left to right, QMF24207, 24204, 24205, 12436, 24203, 24208, 24209, and 24206.

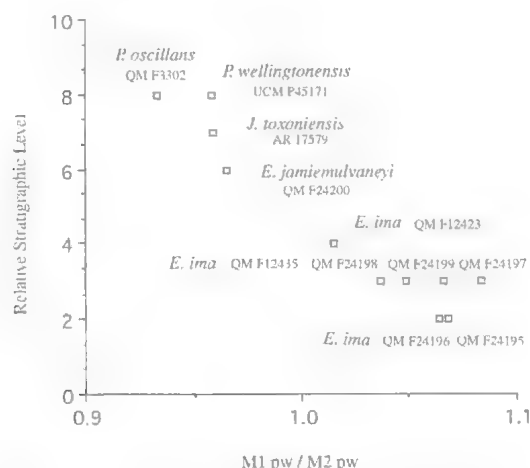


FIG. 7. M_1 pw / M_2 pw vs relative stratigraphic level for propleopines.

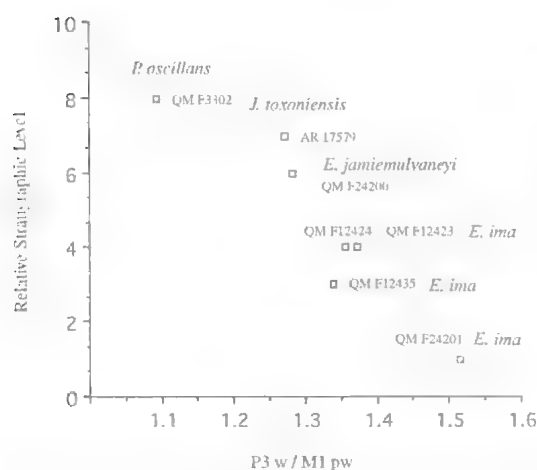


FIG. 8. P_3 w / M_1 pw vs relative stratigraphic level for propleopines.

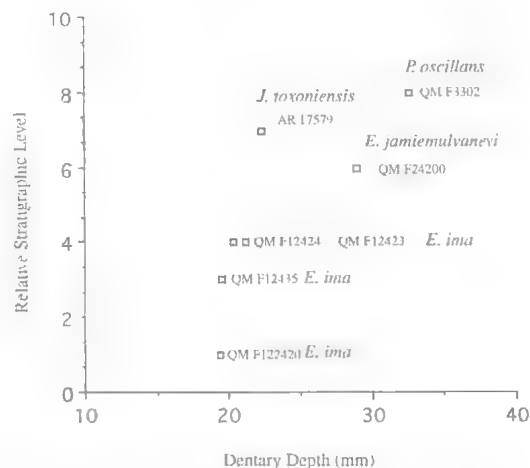


FIG. 9. Depth of dentary vs relative stratigraphic level for propleopines.

congruence between cladistic and stratigraphic arrangements has been demonstrated for many vertebrate taxa by Norell & Novacek (1992a,b), the same authors advised that correlation between the 2 diminishes rapidly where cladistic or stratigraphic data is poorly resolved. Debate over conformity of age and cladistic information commonly centres around the value of superpositional data as an adjunct to phylogenetic reconstruction. Where cladistic analysis is sound it

may be useful as a test of stratigraphic interpretations.

The propleopine phylogeny of Wroe (1996) is based on analysis of an incomplete data matrix, with important characters unknown for several species. Consequently the cladistic data presented cannot be viewed as a robust basis for testing superpositional pattern. However, the productivity of the Oligocene-Miocene deposits of

Riversleigh engenders reasonable expectation for the reliable resolution of phylogenies.

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APPENDIX TO FIGURES 6-9

Data for Fig. 6. M^2 aw divided by M^2 pw (G-value) vs. relative stratigraphic level for propleopines. Measurements in mm. * = skull, (R) = right tooth row, (L) =

Species	Cat. no.	M^2 aw	M^2 pw	G-value	Level
<i>E. ima</i>	QMF24203	6.80	6.10	1.12	3
<i>E. ima</i>	QMF24204	6.80	6.20	1.10	3
<i>E. ima</i> *	(R)QMF12436	6.40	5.80	1.10	3
<i>E. ima</i> *	(L)QMF12436	+	5.90		3
<i>E. ima</i>	QMF24205	6.50	5.90	1.10	3
<i>E. ima</i>	QMF24206	6.80	5.90	1.15	3
<i>E. ima</i>	QMF24207	7.20	6.60	1.09	3
<i>E. ima</i>	QMF24208	6.70	5.90	1.14	3
<i>E. ima</i>	QMF24209	6.20	5.40	1.15	3
<i>E. ima</i>	QMF24210	7.40	6.60	1.12	4
<i>E. ima</i>	QMF24211	6.90	5.80	1.19	6
<i>E. jamiemulvaneyi</i>	QMF24212	6.90	6.60	1.05	6
<i>P. oscillans</i>	QMF6675	9.20	8.70	1.06	8
<i>P. chillagoensis</i>	NMVP15917	10.7	8.70	1.23	8

Data for Fig. 7. M_1 pw divided by M_2 pw (G-value) vs. stratigraphic level. Measurements in mm.

Species	Cat. no.	M_1 pw	M_2 pw	G-value	Level
<i>E. ima</i>	QMF24195	6.70	6.30	1.06	2
<i>E. ima</i>	QMF24196	6.30	5.90	1.07	2
<i>E. ima</i>	QMF24197	6.50	6.00	1.08	3
<i>E. ima</i>	QMF24198	5.70	5.50	1.04	3
<i>E. ima</i>	QMF12435	6.50	6.20	1.05	3
<i>E. ima</i>	QMF24199	6.50	6.10	1.07	3
<i>E. ima</i>	QMF12423	7.00	6.90	1.01	4
<i>E. jamiemulvaneyi</i>	QMF24200	8.20	8.50	0.97	6
<i>P. wellingtonensis</i>	UCMP45171	9.20	9.60	0.96	8
<i>P. oscillans</i>	QMF3302	9.70	10.4	0.93	8
<i>J. toxoniensis</i>	AR17579	7.00	7.40	0.96	7

Data for Fig. 8. P_3 w divided by M_1 pw (G-value) vs. stratigraphic level for propleopines. Measurements in mm.

Species	Cat. no.	P_3 w	M_1 pw	G-value	Level
<i>E. ima</i>	QMF24201	10.3	6.80	1.56	1
<i>E. ima</i>	QMF12435	8.70	6.50	1.34	3
<i>E. ima</i>	QMF12424	8.80	6.50	1.35	4
<i>E. ima</i>	QMF12423	9.60	7.00	1.37	4
<i>E. jamiemulvaneyi</i>	QMF24200	10.5	8.20	1.28	6
<i>P. oscillans</i>	QMF3302	10.6	9.70	1.09	8
<i>J. toxoniensis</i>	AR17579	8.9	7.00	1.27	7

Data for Fig. 9. Depth of dentary vs. stratigraphic level for propleopines. Measurements in mm.

Species	Cat. no.	Dentary depth	Level
<i>E. ima</i>	QMF24201	19.3	1
<i>E. ima</i>	QMF12435	19.4	3
<i>E. ima</i>	QMF12424	21.1	4
<i>E. ima</i>	QMF12423	20.3	4
<i>E. jamiemulvaneyi</i>	QMF24200	28.9	6
<i>P. oscillans</i>	QMF3302	32.6	8
<i>J. toxoniensis</i>	AR17579	23.3	7

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